A Comparative Evaluation of Techniques for Ecological Ordination using Simulated Vegetation Data

and

An Integrated Ordination - Classification Analysis of the Alpine and Subalpine Plant Communitites of the Mt. Field Plateau, Tasmania.

by

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PART 2 An Integrated Ordination - Classification Analysis of the Alpine and Subalpine Plant Communities of the Mt. Field Plateau, Tasmania

ABSTRACT

This thesis consists of two, inter-related sections. In Part 1, the relative utility of ordination techniques, for the purpose of indirect gradient analysis in plant ecology, is studied empirically, using simulated data derived from flexible models of vegetation-gradient relationships. Part 2 is an integrated analysis of vegetation data obtained by intensive sampling of the subalpine and alpine vegetation of the Mt. Field Plateau, Tasmania. The results of the direct gradient analysis of the Mt. Field vegetation were taken into account when formulating the models used in Part 1. In return, the selection of the most appropriate methodology for indirect gradient analysis of the Mt. Field data drew upon the results of the comparative evaluation of techniques in Part 1.

Previous studies which have evaluated the performance of ordination techniques using simulated vegetation data are reviewed. Most such studies have employed models in which the response profiles of species along the artificial gradients were Gaussian. Some preliminary experiments with plausible alternative models have suggested that even the most promising of recently introduced ordination methods may be undesirably sensitive to small variations in the model. Since the available observational evidence does not support the general applicability of the Gaussian model in nature, the relevance of the results of comparative studies based on Gaussian models is in doubt.

Noting that present evidence is insufficient to permit the formulation of a general model of vegetational response to environmental gradients, the present study attempts to identify ordination methods which are robust to variations in those features of the model still subject to debate. A flexible modelling approach was developed, based on the use of beta functions, which can produce unimodal curves of varying skewness. The models allow "competition" between species to be introduced, in the form of linear interaction coefficients, thus producing shouldered, bimodal or multimodal response curves of the types often observed in direct gradient analyses. Both stand abundance (the sum of the abundances of all species present in a sample) and alpha diversity (the number of species per sample) may be varied along gradients in a flexible manner. Quantitative noise may be introduced, in the form of random departures from the expected abundance. Probability of occurrence profiles may optionally be used to introduce qualitative noise. The models allow both unidimensional compositional gradients (coenoclines) and two-dimensional patterns (coenoplanes) to be produced.

Using such models, the relative performance of the ordination techniques Detrended Correspondence Analysis (DCA), "Local" Non-metric Multidimensional Scaling (LNMDS), Principal Co-ordinates Analysis (PCoA), Principal Components Analysis (PCA) and Gaussian Ordination (GO) was assessed. Ordination configurations were rotated to best fit with the original arrangement of samples along the simulated gradient(s) using Procrustean analysis, and the RMS displacement error was used as a measure of ordination efficacy. For ordinations of coenoclines, the

Kendall rank correlation coefficient was used to assess the accuracy with which the rank order of samples was recovered. Experiments were performed on the effects of variation in several properties of the models, with particular attention being devoted to the robustness of methods to variations in the shape of response curves, the introduction of noise and the arrangement of samples.

Experiments with coenocline models confirmed the ineffectiveness of PCA, except when the beta diversity of the gradient is low (no more than 4Z). PCoA, operating on a percentage similarity matrix, was similarly affected. With models containing only unimodal curves, DCA was generally the most successful of the methods compared. GO was able to improve significantly on the DCA solutions only when beta diversity was less than 6Z, quantitative noise levels were low and the curves were not grossly skewed. When models included shouldered and bimodal curves, LNMDS was consistently superior to DCA and GO.

PCA and PCoA ordinations of simulated coenoplanes were poor unless the beta diversity of both gradients was low. With "rectangular" coenoplanes, curvilinear distortion of the longer gradient often obscured variation related to the secondary gradient. LNMDS consistently improved on DCA solutions for all the coenoplane models examined. The DCA results, even with noiseless data from some of the symmetrical, unimodal models, were occasionally very poor. Neither LNMDS nor DCA gave consistently satisfactory results when coenoplanes were sampled with cross-shaped or T-shaped sampling patterns, which simulate field situations where one gradient is expressed only in a restricted region of another gradient.

The present study suggests a preference for LNMDS as a "general purpose" approach to indirect gradient analysis. However, practical limitations of LNMDS may make DCA the method of choice when the number of samples is large. Significant advances in the methodology of indirect gradient analysis are unlikely to be made until much more observational evidence concerning the nature of vegetational response to environmental gradients is available.

Subalpine and alpine vegetation on the Mt. Field Plateau, a dolerite capped horst in south-central Tasmania, was intensively sampled using a stratified, systematic arrangement of 438, 100 sq. m quadrats. In each sample, cover estimates were made for all vascular plant species and various site and community characteristics were recorded.

A direct gradient analysis was performed, using altitude and substrate drainage (estimated on a five point scale) as axes. The response surfaces for mean cover of 111 species were predominantly unimodal (80%), although only 45% appeared to be symmetrical. For the unimodal species, the distribution of modes over the ecoplane was consistent with random expectation. The frequency distribution of response surface maxima was approximately lograndom for non-woody species, but the distribution for woody species did not fit lograndom or lognormal hypotheses.

Mean values of community characteristics, such as height of tallest stratum, total cover and alpha diversity, displayed systematic

trends in relation to altitude and drainage. The pattern of alpha diversity was further clarified by the division of species into growth-form groups. Beta (between-habitat) diversity along the drainage gradient showed a consistent decline with increasing elevation.

The potential value of Generalised Linear Modelling (GLM) as a more rigorous approach to the fitting of response surfaces was examined for a selected set of 18 dominant species. An initial qualitative model was fitted, in order to identify samples where the expected probability of occurrence of a species was low. Such samples were then omitted when fitting a predictive model for percentage cover. For all but four of the species, probability of occurrence was adequately fitted by a symmetrical, bell-shaped surface. The quantitative (percentage cover) models for most species had low adjusted r-squared values, indicating a relatively large amount of "noise" variation. The factors which may have contributed to this noise variation are discussed.

Because of the large number of samples, which made LNMDS impracticable, DCA was adopted as a primary approach for indirect gradient analysis. The first two axes of a DCA ordination, based on cover class data, defined a coenoplane to which altitude and drainage were strongly related. This result supports the choice of these two complex-gradients as axes for direct gradient analysis. The third axis was a spurious "interaction" axis, resulting from the failure in DCA to detrend the third and subsequent axes with respect to combinations of the previously extracted axes. The fourth axis represented a compositional gradient among subalpine forests on well drained sites, which was tentatively related to firing history.

DCA based on presence-absence data gave very similar results, indicating that, at these levels of beta diversity, most of the relevant information concerning the positions of samples on the major underlying gradients is contained in the qualitative component of the data. A DCA ordination of percentage cover data (i.e. midpoints of cover classes) produced a distorted reconstruction of the altitude X drainage coenoplane, with one corner projected into a third dimension. The origin of this type of distortion, which was also noted with some of the coenoplane models in Part 1, is not clear.

A compound data set was produced by forming the centroids of 60 Minimum Sum-of-Squares clusters. Ordinations of this compound data set by various techniques, including DCA, local and global NMDS, PCoA and PCA, were compared. The ineffectiveness of PCoA and PCA was readily apparent. Curvilinear distortion of the altitude X drainage coenoplane prevented adequate recovery of the tertiary "firing history" gradient. The NMDS solutions based on local and global criteria were very similar to each other and they differed from the DCA result only in local details.

Both direct and indirect gradient analyses indicated that the vegetation of the Mt. Field Plateau forms a compositional continuum, with species having individualistic ecological response surfaces in relation to altitude and drainage. However, dissection of the continuum into a relatively small number of reference classes or noda was considered desirable for the purpose of synoptic description. Numerical classifications of the samples were performed using several techniques. The 21 group solution produced by Minimum Sum-of-Squares Clustering, followed by iterative relocation, was considered most useful. The species were also classified, using the TWO-STEP dissimilarity coefficient and the flexible beta sorting strategy. A species classification based on cover class data, normalised by species, was found to be most satisfactory. Ordered two-way tables, in which noda were arranged, as far as possible, in altitudinal series within drainage groups, and species were sorted into groups defined by TWO-STEP, provided a powerful summary of the major features of the vegetation pattern on the Mt. Field Plateau. The present study illustrates the value of an integrated approach to the descriptive analysis of vegetation.

PART 1

A Comparative Evaluation of Techniques for Ecological Ordination using Simulated Vegetation Data

CHAPTER 1 : THE COMPARATIVE EVALUATION OF ORDINATION METHODS USING SIMULATED VEGETATION DATA : A REVIEW

1.1 Introduction

Multivariate methods of the type generally known as "ordination" (Goodall 1954a) are widely used by plant ecologists and phytosociologists as research tools in the study of vegetation (Mueller-Dombois and Ellenberg 1974; Orloci 1978a). Such techniques seek to arrange the entities or units of interest (e.g. quadrats, releves, species) in uni- or multidimensional series, as opposed to "classifications", which organise the units into classes. In general, ordinations emphasise the continuous aspects of variation among the units, whereas classifications tend to concentrate on discontinuity. Nevertheless, ordination and classification are best regarded as alternative, potentially complementary approaches to data analysis, rather than antagonistic and mutually exclusive strategies (Goodall 1954b; Whittaker 1972a).

The term "ordination" has been applied to a wide variety of methods in plant ecology. These range from the simple graphing of vegetation samples with respect to axes representing environmental variables, to the arrangement of vegetation samples on abstract compositional axes, extracted from data on the occurrences or abundances of species in the samples. Austin (1968) proposed that the terms "vegetational ordination" and "environmental ordination" be used for approaches which arrange samples according to vegetational and environmental similarities respectively. Similarly, Whittaker and Gauch (1978) distinguished "indirect ordination" and "direct ordination".

Most published applications of vegetational ordination (see numerous references in Orloci 1978a) attempt to relate the patterns of compositional variation revealed by ordination to gradients in environmental variables, thus implying an emphasis on the trend-seeking objective. Authors such as Austin (1976a) and Noy-Meir and Whittaker (1977) clearly regard the elucidation of relationships between environmental gradients and trends in community composition as the major goal in vegetational ordination, and this view is shared by the present author. However, early discussions of ordination in plant ecology (e.g. Orloci 1966; Anderson 1971) often stressed the efficient reduction of dimensionality (i.e. summarisation). This emphasis may have reflected a belief that parsimonious summarisation would invariably lead to an ordination in which interesting trends or patterns of variation were revealed most clearly. Subsequent work, to be discussed later in this chapter, has suggested that this notion is not well founded.

If the recovery of information about underlying environmental relationships is accepted as a major purpose of vegetational ordination, a number of approaches to the comparative evaluation of techniques are possible. One such approach is to compare the results of applying different ordination methods to sets of field data (e.g. van Groenewoud 1965; Austin and Orloci 1966; Bannister 1968; Chardy, Glemarec and Laurec 1976; Prentice 1977; Brown, Ratkowsky and Minchin 1983; Oksanen 1983). The major limitation of such studies is that the underlying gradient structure, which a "successful" ordination method is expected to recover, is usually known only approximately. Hence a detailed assessment of the relative performance of different ordination

techniques is not possible. The effects of minor environmental factors and stochastic variability associated with historical events and sampling errors may obscure relationships between the vegetation and major underlying gradients in many sets of field data.

An alternative approach involves the comparison of vegetational ordinations with direct ordinations based on environmental variables thought to be of major importance in influencing vegetation patterns (Jeglum, Wehrhahn and Swan 1971; Westman 1975; del Moral 1980). However, it is often extremely difficult, if not impossible, to identify an environmental variable which is susceptible to measurement and effectively expresses the dynamic complexity of inter-related factors which characterises most major environmental gradients. Furthermore, there is no guarantee that the axes chosen for direct ordination do indeed represent the only important determinants of vegetational composition.

A third approach to the comparative evaluation of methods for vegetational ordination was pioneered by Swan (1970). He constructed simplified models of the response of species to a single environmental gradient and examined the accuracy with which a particular ordination method recovered the unidimensional gradient structure from data sets obtained by sampling the models. This work has stimulated a series of studies in which simulated data sets are used for the comparative evaluation of ordination methods (Noy-Meir and Austin 1970; Austin and Noy-Meir 1971; Gauch and Whittaker 1972a,b, 1976; Kessell and Whittaker 1976; Austin 1976a,b; Fasham 1977; Gauch, Whittaker and Wentworth 1977; Prentice 1980; Gauch, Whittaker and Singer 1981; Mohler 1981).

The general strategy used in such studies may be summarised as follows :

(1) Construct a plausible model of the manner in which the abundances of species vary along one or more environmental gradients. For each species, define an ecological response curve (surface), relating its abundance to position on the gradient(s).

(2) Sample the model at several points. The abundance of each species in a given sample is given by the height of its response curve (surface) at that point. A degree of "noise" may be introduced by adding a random error component to the expected abundances.

(3) Subject the simulated data matrix to ordination by each of several techniques.

(4) Examine the ordinations and compare their relative success in recovering the underlying gradient structure built into the model. A successful ordination is defined as one in which the relative positions of the samples accurately reflects their relative locations along the simulated environmental gradient(s).

The use of simulated, rather than real, vegetation data has the advantage that the expected result of a successful ordination can be specified precisely. Various data set properties can be varied independently, in order to study their effects on the performance of different ordination techniques. However, the relevance of the results of such simulation studies is entirely dependent on the extent to which the models employed are acceptable simplifications of the complex relationships between plant communities and environmental gradients which occur in nature. Part 1 of this thesis is a further contribution to this area of research. A review of the methodology and major results

of previous work in the field follows (see also Whittaker and Gauch 1978).

1.2 Vegetation-Gradient Models

The first study in which artificial data from vegetation models were used to evaluate the performance of an ordination method was that of Swan (1970). While recognising the complexity of relationships between natural communities and environmental gradients, Swan chose, as a first approximation, to work with very simple models of the compositional trend along a single gradient. The relationship between the abundance of a species in a sample and the position of that sample on the gradient was represented by a symmetrical, bell-shaped curve. In each model, the abundance profiles for all species had the same height at the mode and spanned an equal range of the gradient. The modes of species were evenly spaced. A series of models with increasing beta diversities (i.e. degrees of compositional change along the gradient) was constructed by reducing the range of the abundance profiles used in each model. The effect of adding extra species at each end of the gradient, with modes located at equal intervals outside the sampled region of the gradient, was also examined. The tails of the response curves for such species extended into the sampled region as S-shaped curves. In all his experiments, Swan placed samples at equidistant points along the artificial gradient. The abundance of each species in a given sample was determined by the height of its response curve at that sampling point.

Austin and Noy-Meir (1971) extended the modelling approach to two dimensions, producing models in which the responses of species to two

gradients were represented by Gaussian surfaces. The abundance, Y, of a species at a given point on the "ecoplane" defined by the two gradients was given by the equation

$$Y = YO.e^{(-D^2/K)} \qquad (1)$$

where YO is the abundance of the species at its mode, D is the distance between the sampling point and the position of the mode and K is a constant controlling the "width" (standard deviation) of the Gaussian surface. The tails of the response surfaces were truncated, by replacing values less than unity by zero.

In one set of models, all species were given equal maxima (YO=100) and their modes were located at points equally spaced on a 5 X 6 grid with respect to the two gradients. Samples were placed at the same 30 points. Different models in this set were used to investigate the effects of (a) varying the widths of response curves (and hence the beta diversities of the two gradients) and (b) the addition of extra species with modes outside the edges of the sample grid or near its centre. In another model, the modes of 30 species were located at random within a square, and their maxima (YO) and width parameters (K) were selected at random, each from among three possible values. This model was sampled using 30 points placed at random on the plane defined by the two gradients.

Gauch and Whittaker (1972a) developed a computer program for the simulation of the gradient in communities ("coenocline" of Whittaker 1960) along a single environmental gradient. Their approach to the simulation of coenoclines was based on a set of nine assumptions or

hypotheses regarding the relationships between plant communities and environmental gradients, which were derived from an informal study of the results of direct gradient analyses (Whittaker 1956,1960,1967; Whittaker and Niering 1965). These were as follows :

(1) The response curves of species along an environmental gradient are Gaussian in form. The abundance, Y, of a species at a point X on a gradient is given by

$$Y = YO.e^{-(X-M)^2/2S^2} \qquad (2)$$

where YO is the abundance of the species at its mode, M is the position of the mode on the gradient and S is the standard deviation of the response curve.

(2) The optima or modes (M) of minor species are scattered at random along gradients, while those of major species tend to be more uniformly dispersed.

(3) When the set of species occurring along an environmental gradient is considered, the frequency distribution of the maxima of their response curves (YO) is often either lograndom or lognormal.

(4) The standard deviations (S) of the response curves of species are normally distributed, with a standard deviation equal to about 0.3 times the mean value.

(5) The values of the three parameters (YO,M,S) defining the response curves of each species are not correlated between species.

(6) The sum of the abundances of all species at a given point on the gradient may be limited by an "environmental carrying capacity". The program incorporates an option which allows the abundances of all species to be adjusted such that their sum in each sample is equal to some specified constant value.

(7) The tails of the Gaussian curves are truncated at some small abundance value.

(8) Coenoclines differ in (a) the average number of species per sample (alpha diversity), (b) the degree of compositional change or species turnover along the gradient (beta diversity) and (c) total species richness (gamma diversity).

(9) Field data usually contain quantitative sampling errors or "noise".

The computer program which embodies these assumptions is part of the Cornell Ecology Programs Series (Gauch 1979). The exposition of the approach by Gauch and Whittaker (1972a) includes an appendix describing the various options available in the program.

Coenoclines produced by the program are 100 arbitrary units in length. Beta diversity is controlled by an input parameter, Z, which determines the average value of the standard deviation (S) of the response curves of species. The average standard deviation of the response curves is equal to 100/Z. Small values of Z produce broad abundance profiles and hence low beta diversity, while large values produce narrow profiles and high beta diversity. The coenocline is extended at each end by an amount equal to five average standard deviations (500/Z) for the allocation of species modes (M). This avoids "edge effects" which would occur if all species modes were placed inside the sampled region of the coenocline (0 to 100).

The value of the parameter Z is a measure of the total "length" of the coenocline, the unit of measurement being the average standard deviation of the Gaussian response curves. Whittaker (1956,1960)

developed an alternative unit to measure the beta diversity of coenoclines. This is the "half-change" (HC), defined as the average distance along a coenocline between samples whose compositional similarity (as expressed by a chosen similarity coefficient) is half that of replicate samples from the same position on the gradient. Gauch (unpublished results reported in Gauch and Whittaker 1972a) has determined that, for simple noiseless coenoclines (in which the values of YO and S are identical for all species, and modes, M, are evenly spaced), one half-change of the percentage similarity coefficient (Appendix A, equation A1) is equivalent to about 1.35 Z units.

Gauch and Whittaker (1976) extended their modelling approach to allow the simulation of two-dimensional community patterns or "coenoplanes". Their programs for coenoplane simulation were based on a set of 12 assumptions, most of which were two-dimensional analogues of those used for coenocline simulation.

The response surfaces of species were assumed to be of Gaussian form. The abundance, A, of a species at a point on the coenoplane with co-ordinates (X,Y) was given by

$$A = AO.e^{-[\,(X-Mx)^2/2Sx^2 + (Y-My)^2/2Sy^2\,]} \qquad (3)$$

where AO is the abundance of the species at its mode, Mx and My are the co-ordinates of the mode on the two axes of the coenoplane and Sx and Sy are the standard deviations of the Gaussian surface along the two coenoplane axes. The response surface may be rotated with respect to the coenoplane axes through an angle θ. The program allows these angles of rotation to be normally distributed about some mean value or randomly distributed. Alternatively, the values of θ for all species may be set

at zero. Values for the other parameters of the response surfaces (AO,Mx,My,Sx,Sy) are allocated using principles similar to those used in the coenocline simulation program described above.

The placement of samples on the coenoplane may be either uniform (on a regular grid), random or deliberate. Uniform or random patterns may be modified by restriction to specified parts of the coenoplane and/or concentration, which produces linear variation in sample density along the coenoplane axes.

A suite of programs which produce simulated coenoplane data according to these principles is part of the Cornell Ecology Programs Series (Gauch 1979). Gauch, Whittaker and Singer (1981) have reported extensions of their modelling approach to three and four dimensions. Response hypersurfaces, relating the abundances of species to three or more environmental gradients, are defined using Gaussian functions. However, computer programs for these multidimensional Gaussian models are not yet widely available.

Gaussian coenoclines and coenoplanes produced by the programs of Gauch and Whittaker (1972a,1976) have been employed in nearly all of the subsequent studies which have compared ordination techniques using artificial data. The major exception is the work of Austin (1976a,b). Austin (1976a) questioned the assumption that the abundance profiles of species along environmental gradients are Gaussian in form. He presented evidence that many response curves observed in direct gradient analyses are either skewed, shouldered, bimodal or multimodal. Two alternative coenocline models were suggested.

In the first, the response curves of species were represented by beta functions, which are defined by the equation

$$f(X) = X^{\alpha}.(1-X)^{\gamma} \qquad 0 \leqslant X \leqslant 1 \qquad (4)$$

Response curves described by beta functions can assume a variety of forms, depending on the values given to the powers α and γ. When α and γ are positive and equal the curves are unimodal and symmetrical. Unequal positive powers produce skewed curves. Austin (1976a) allocated values of α and γ arbitrarily, to produce a model in which the response curves of species were unimodal, but of varying skewness.

The second model proposed by Austin (1976a) will be termed the "ecological response" model. This model represented an attempt to incorporate the effects of interspecific competition and variation in "environmental carrying capacity" along a gradient. Experiments in which plant species were grown along contrived environmental gradients, both in monoculture and in admixture (e.g. Ellenberg 1953,1954; Mueller-Dombois and Sims 1966; Austin and Austin 1980), suggest that the form of response curves may be modified by competitive interactions between species. It is thus necessary to distinguish the "physiological response" of a species grown in monoculture from its "ecological response" when in competition with other species along a gradient (Mueller-Dombois and Ellenberg 1974: pp.344-351).

Austin (1976a) defined skewed physiological response curves for each species using simple polynomial equations. Interspecific competition was then introduced by specifying linear interaction coefficients between each pair of species. In each sample, the abundance of a given species, i, was reduced by the sum of products of

the abundances of each other species, j, and the interaction coefficients between species i and j. Finally, the total abundance at each point on the gradient was assumed to be limited by an environmental carrying capacity, which varied systematically along the gradient. The model specified a quadratic relationship between carrying capacity and the gradient, although it was recognised that such a simple relationship is unlikely in nature. Abundances of all species at a given point on the gradient were proportionally adjusted, after correction for competition, such that their total was equal to the carrying capacity at that point.

Austin (1976b) used simulated coenoclines based on the beta function and "ecological response" models in a comparative study of ordination techniques. He did not generalise the approaches to allow the simulation of non-Gaussian coenoplanes.

1.3 Assessment of Fit

When data derived by sampling an artificial coenocline or coenoplane is subjected to ordination, the "success" of the ordination, for the purpose of indirect gradient analysis, may be defined as the accuracy with which the positions of the samples in the ordination reflect their locations in the "ecological space" represented by the axes of the coenocline or coenoplane. There need not be a one-to-one correspondence between ordination axes and underlying gradients. The ordination axes may be individually or collectively oblique to these gradients, but the relative positions of samples should be faithfully recovered (Austin 1976a; Whittaker and Gauch 1978).

Various criteria have been used to assess the fit between ordination configurations and the positions of samples on the simulated gradients. The simplest approach is a subjective visual comparison of the ordination of the samples with their expected arrangement (Swan 1970; Noy-Meir and Austin 1970; Austin 1976b; Prentice 1980). Systematic distortions of the underlying gradient structure can be readily appreciated on inspection and gross differences in the performance of methods may be detected. However, precise comparison of the performance of different techniques requires an appropriately defined measure of fit.

Austin and Noy-Meir (1971) computed the squared correlation between inter-sample distances on their model coenoplanes and the corresponding distances on the first two ordination axes. This is a measure of the proportion of the "ecological distances" accounted for by the ordination. Gauch, Whittaker and Singer (1981) used the square root of this measure, the so-called matrix correlation (Sneath and Sokal 1973), but found it deficient in two respects. Firstly, a given value may be the result of a few large displacements or many small ones. Secondly, the measure is rather insensitive, since high values may be obtained with relatively coarse agreement between the two configurations.

Gauch and Whittaker (1972b) employed two performance statistics. The first (r) was the Pearson product-moment correlation coefficient computed between the co-ordinates of samples on the first axis of an ordination and their known positions along the model coenocline. This was intended as a measure of the accuracy with which sample positions were recovered. The second statistic (P) was the mean perpendicular

distance of points from the first ordination axis divided by the length of the axis, a measure of "spurious information". A consideration of some simple examples (Table 1.1) shows that the correlation coefficient, r, is not really suitable as a goodness-of-fit measure. In column one of the table, the positions of 21 samples, evenly spaced along a coenocline axis 100 units in length, are listed. In columns two to five the co-ordinates of the same samples on the first axis of four hypothetical ordinations are shown. In each case the value of r computed between the ordination co-ordinates and the true sample positions is greater than 0.88, even though only the first of these ordination results would be regarded as a reasonable representation of the relative positions of samples in the model.

Kessell and Whittaker (1976) assessed the accuracy of the recovery of sample positions using the "mean displacement error". This was defined as the mean distance between the locations of samples on the first ordination axis and their positions along the simulated coenocline axis, after the lengths of both axes had been adjusted to 100 units. The mean displacement error has since been used in several studies (Gauch, Whittaker and Wentworth 1977; Mohler 1981; Gauch, Whittaker and Singer 1981). It is only applicable to unidimensional models. An undesirable feature of the measure is that the ordination co-ordinates are brought into correspondence with the true sample positions purely by aligning the two extreme samples on each axis. The measure is thus unduly sensitive to the manner in which those two samples at opposite extremes of the first ordination axis are placed relative to the remaining samples.

Actual Sample Locations	Hypothetical Ordination Results			
	1. Correctly ordered but randomly spaced	2. Central samples bunched	3. Samples polarised at ends and centre	4. Samples polarised at extremes
0	0	0	0	0
5	5.9	10	0	0
10	9.2	20	0	0
15	12.8	30	0	0
20	17.1	40	0	0
25	23.6	50	0	0
30	27.8	50	0	0
35	33.1	50	50	0
40	36.5	50	50	0
45	44.1	50	50	0
50	51.2	50	50	50
55	58.7	50	50	100
60	67.2	50	50	100
65	70.7	50	50	100
70	73.4	50	100	100
75	73.7	50	100	100
80	79.8	60	100	100
85	83.4	70	100	100
90	90.8	80	100	100
95	99.4	90	100	100
100	100.0	100	100	100
Product-moment correlation (r) of ordination co-ordinates with true sample positions	0.996	0.893	0.944	0.886

Table 1.1 An illustration of the insensitivity of the product-moment correlation coefficient as a measure of the accuracy of sample position recovery by an ordination. Very poor ordinations, such as 2, 3 and 4, can nevertheless produce correlations greater than 0.88.

A better measure, which is easily generalised to several dimensions, was employed by Fasham (1977). For a k-dimensional model, the configuration of samples on the first k ordination axes is first fitted to the configuration of samples with respect to the simulated gradients, using the technique of Procrustean analysis (Schonemann and Carroll 1970). This procedure fits one configuration to another by translation of the origin, rigid rotation and possible reflection of axes and uniform expansion or contraction of scaling, so as to minimise the sum of squared distances between corresponding points in the two configurations. The square root of the mean squared displacement of each sample point in the fitted ordination from its position in the model is then used as a goodness-of-fit statistic, the "RMS displacement error". Procrustean analysis is illustrated, with the aid of an example, in section 2.2. In contrast to the mean displacement error of Kessell and Whittaker (1976), the RMS displacement error obtained by Procrustean analysis takes into account the positions of all samples when bringing the two configurations into optimal agreement, rather than just the two extreme samples.

For coenocline models, a minimal requirement for a successful ordination is that the rank order of samples along the gradient is faithfully recovered. Fasham (1977) used the Kendall rank correlation coefficient (Kendall 1938) as a measure of rank order recovery. This statistic appears to be a useful measure of the degree of agreement between two orderings. Gauch, Whittaker and Wentworth (1977) recorded the percentage of sequence reversals between consecutive samples for a similar purpose, while Austin (1976b) simply noted the success or failure of rank order recovery.

community). The CD measure is the qualitative equivalent of PD. The effect of beta diversity was examined using simulated coenoclines with beta diversities ranging from 2.5 to 30Z. For coenoclines with a beta diversity of 6Z, the effect of adding quantitative sampling errors was studied, using noise levels ranging from 0.1 to 0.5 in the "F" units of Gauch and Whittaker (1972a). A noise level of 0.25F produces an average percentage similarity between replicate samples, or "internal association", of about 70 percent, while a noise level of 0.5F reduces the internal association to about 55 percent. Samples in all experiments were evenly spaced along the simulated coenoclines. For the Polar Ordination, Similarity Projection and Importance Projection techniques, samples located at opposite extremes of the simulated coenoclines were selected as ordination poles.

Noy-Meir (1974a) applied Parametric Mapping, with a number of different option settings, to simulated data from a simple Gaussian coenocline of Swan (1970) and one of the coenoplane models of Austin and Noy-Meir (1971).

The ordination methods compared by Kessell and Whittaker (1976) were Principal Components Analysis (PCA), Polar Ordination (PO) and Discriminant Function Analysis. PO was applied using Euclidean distance (ED), percentage difference (PD) and CD (the complement of the Sorenson coefficient) as distance measures. A set of nine Gaussian coenoclines, representing all factorial combinations of three levels of beta diversity (3, 6 and 12Z) and three levels of sampling error (corresponding to internal associations of 100, 85 and 70 percent), was created. The entire set was replicated, giving 18 models in all. Each

coenocline was sampled using 50 equally spaced samples and the resulting data sets were ordinated by each method. The effects on PCA of (a) using different numbers of evenly spaced samples and (b) clustering samples in certain parts of the coenocline were also examined.

Austin (1976b) compared Reciprocal Averaging (RA), Parametric Mapping, Gaussian Ordination (GO) and "Global" Non-metric Multidimensional Scaling (GNMDS). The primary objective of the study was to assess the robustness of the techniques to moderate variations in the generating model, particularly the shape of response curves. The four models employed were (a) a coenocline with bell-shaped, symmetrical response curves (model 5 of Swan 1970), (b) a coenoplane with Gaussian species response surfaces (model 1A of Austin and Noy-Meir 1971), (c) a coenocline in which species abundance profiles were generated using arbitrary beta functions and (d) a coenocline based on the "ecological response" model described by Austin (1976a).

The study of Gauch, Whittaker and Wentworth (1977) compared Reciprocal Averaging (RA), PCA (unstandardised, centred by species) and Polar Ordination (PO) using the percentage difference measure (PD), and included some supplementary experiments involving variants of these methods. The effect of beta diversity was examined using Gaussian coenoclines ranging in length from 0.3 to 20 half-changes (HC) in percentage similarity. Three levels of sampling error, corresponding to internal associations of 100, 90 and 75 percent, were studied using coenoclines with beta diversities ranging from 1 to 10HC. To examine the effect of secondary gradients, Gaussian coenoplanes with beta diversities ranging from 0.7 to 10HC were employed. Each coenoplane was sampled at 40 points arranged on a regular 8 X 5 grid. The

consequences of sample clustering were studied using coenoplanes of 4.5 X 1.5HC and 2.5 X 1.5HC. These coenoplanes were initially sampled using 20 points on a regular 5 X 4 grid, and one or two clumps of five samples were then added. Simulated outliers or deviant samples of two different kinds (see section 1.5.3.4) were added to some data sets, in order to assess their impact on ordinations. The vulnerability of ordinations to the effects of partial disjunctions (where sub-sets of the data have few species in common) was studied by removing adjacent groups of samples from a simple 10HC coenocline.

Fasham (1977) used data from simulated Gaussian coenoclines of length 2.25, 4.5, 9 and 22HC to compare the effects of increasing beta diversity on the performance of Principal Components Analysis (PCA), Reciprocal Averaging (RA) and "Global" Non-metric Multidimensional Scaling (GNMDS). PCA and RA ordinations were used to supply starting configurations for GNMDS, which was performed in both one and two dimensions. The 4.5HC coenocline was also ordinated using non-centred PCA and GNMDS with a variety of similarity coefficients and data transformations. Simulated Gaussian coenoplanes of 1.5 X 1.5HC, 4.5 X 1.5HC and 4.5 X 4.5HC were used to compare the performance of PCA, RA and GNMDS in the presence of two underlying gradients. Prentice (1980) used the same simulated data sets as Fasham (1977) to assess the relative performance of several forms of Non-metric Multidimensional Scaling ("global" v. "local" scaling and primary v. secondary treatment of tied similarities).

Gauch, Whittaker and Singer (1981) compared Reciprocal Averaging (RA), Detrended Correspondence Analysis (DCA), Parametric Mapping,

several types of Non-metric Multidimensional Scaling (both "global" and "local" forms) and Gaussian Ordination, the latter on unidimensional models only. Simulated Gaussian coenoclines with lengths of 3, 5, 7 and 10HC were used to assess the effects of increasing beta diversity. Coenoplanes of 1.5 X 1.5, 4.5 X 1.5 and 4.5 X 4.5HC were used to study the effects of secondary gradients. More complex data sets, derived from Gaussian models with up to four gradients, were also studied. In order to compare the vulnerability of the ordination methods to noise variation, quantitative sampling errors were added to some data sets. The noise levels which were employed produced internal associations of 85 and 60 percent.

The study of Mohler (1981) compared the effects of different sampling arrangements along simulated Gaussian coenoclines on the performance of Detrended Correspondence Analysis (DCA), Reciprocal Averaging (RA) and Principal Components Analysis (PCA). Samples were either evenly spaced, concentrated towards the extremes of the coenocline or concentrated in the middle of the coenocline.

1.5 Summary of Major Results

1.5.1 Coenoclines with Gaussian Response Curves

1.5.1.1 Beta Diversity

Swan (1970), working with a variety of Polar Ordination, found that his simple coenoclines were represented as curves in the space defined by the first three ordination axes. With increasing beta diversity, the curvature became more pronounced and the extremes of the coenocline were folded in towards the centre of the ordination. This involution resulted in the failure of the ordination to recover the

correct rank order of samples on the first axis. Noy-Meir and Austin (1970) applied the more widely used technique of Principal Components Analysis (PCA) to Swan's models and noted a similar effect, although the PCA ordinations of the models with highest beta diversity were somewhat less involuted than those produced by Swan's method.

Gauch and Whittaker (1972b) found that increasing beta diversity adversely affected the results of all ordination methods tested. Techniques using Euclidean distance (ED) as a measure of sample dissimilarity were most vulnerable to curvilinear distortion and involution, while Polar Ordination using percentage difference (PD) or its binary equivalent (CD) performed best. Kessell and Whittaker (1976) obtained similar results. They found that Polar Ordination (PO) using the PD measure was less affected by increasing beta diversity than PO with CD, PO with ED and Principal Components Analysis (PCA). However, even PO with PD was ineffective at beta diversities above about 5 half-changes (HC), at which point the extremes of the coenocline have no species in common.

Gauch, Whittaker and Wentworth (1977) found that Reciprocal Averaging (RA) was resistant to involution, even at very high beta diversities, although there was an increasing tendency for samples to be concentrated towards each end of the first axis as beta diversity increased. RA was found to be affected by curvilinear distortions analogous to those affecting PCA, but less severe. In RA ordinations of coenoclines, scores on the second axis bore an approximately quadratic relationship to those on the first axis. Polar Ordination (PO) with the percentage difference measure (PD) performed nearly as well as RA up to

beta diversities of about 5HC, while PCA (unstandardised, centred by species) was subject to involution above 3HC. Standardisation by species standard deviation reduced the curvilinear distortion in PCA ordinations and extended the range of beta diversity which could be ordinated without involution.

Fasham (1977) found PCA to be more prone to the curvilinear distortion of coenoclines with increasing beta diversity than Reciprocal Averaging (RA) and Global Non-metric Multidimensional Scaling (GNMDS). RA always recovered the correct rank order of samples on the first axis, even up to 22HC. However, at high beta diversities there was a tendency for samples to have a clumped distribution along the axis, instead of the expected even spacing. As observed by Gauch, Whittaker and Wentworth (1977), the approximately quadratic arch, relating scores on the second RA axis to those on the first, became more pronounced as beta diversity increased. Unidimensional GNMDS ordinations were consistently less distorted than both RA and PCA ordinations. The recovery of sample order was perfect up to 22HC. When two dimensions were allowed for GNMDS, the coenoclines were curved into the second dimension and the recovery of the rank order of samples on the first ordination axis was no longer perfect.

Noy-Meir and Austin (1970) recognised that the curvilinear distortion of coenoclines by PCA was a consequence of the incompatability of the linear model implicit in PCA and the non-linear structure of the simulated data. The axes in PCA are linear combinations of the original variables (i.e. species abundances). Hence the compositional sequence along an environmental gradient will only appear as a linear trend in a PCA ordination if the relationships

between the abundances of species and position on the gradient are linear. In a Gaussian coenocline of moderate to high beta diversity these relationships are not even monotonic, let alone linear.

The configuration of samples with respect to the first k axes of a PCA ordination is such that the distances between each pair of samples in the ordination reflect their compositional dissimilarities (as expressed by the Euclidean distance metric) as faithfully as it is possible to do so in k dimensions. For Gaussian coenoclines, the non-linearity of the response curves and the truncation of species abundances at zero combine to produce a strongly curved relationship between compositional dissimilarity (Euclidean distance) and ecological distance (i.e. the separation of samples along the gradient) (Swan 1970; Gauch 1973a; van Groenewoud 1976). The Euclidean distance (ED) between two samples which are two units apart on the gradient is less than twice the ED between samples whose separation is one unit. Consequently, a spatial arrangement of the samples which is compatible with the ED values for all pairs of samples must be curved, rather than straight. Standardisation by species, or double standardisation reduces the degree of curvilinear distortion of coenoclines in PCA ordinations by decreasing the curvature of the relationship between ED and the separation of samples along the gradient.

Potential problems in the interpretation of vegetational ordinations by PCA, when species do not respond linearly to underlying gradients had been anticipated previously (Goodall 1954a; van Groenewoud 1965; Austin 1968). However, the full significance of the problem was not realised until the development of the simulation approach. It is

now realised that the curvilinear distortion of underlying gradients, due to the intrinsic non-linearity of vegetation data, is not peculiar to PCA, but is a general problem with all ordination methods which assume a linear relationship between sample resemblance and gradient separation (e.g. Polar Ordination, Principal Co-ordinates Analysis).

In common with Euclidean distance, dissimilarity measures such as percentage difference (PD) and its binary equivalent (CD) have non-linear relationships with the separation of samples along coenoclines (Gauch 1973a). However, these relationships are not so strongly curved as the relationship for Euclidean distance (ED). This explains the observations of Gauch and Whittaker (1972b) and Kessell and Whittaker (1976), that Polar Ordinations using the PD or CD measures were less affected by curvilinear distortion at a given level of beta diversity than ordinations of the same data sets using ED.

1.5.1.2 Noise

Gauch and Whittaker (1972b) studied the effect of adding noise to data from coenoclines with a beta diversity of 6Z (4.4HC). Polar Ordination (PO) with the percentage difference measure (PD) was least affected, followed by PO and PO variants with Euclidean distance (ED), while ordinations by Principal Components Analysis (PCA) were most strongly affected. They suggested that the greater vulnerability to sampling errors of methods using ED (including PCA) resulted from the squaring of differences in abundance involved in the computation of ED. This tends to give high weight to sampling errors for species which attain high abundances.

Kessell and Whittaker (1976) and Gauch, Whittaker and Wentworth

(1977) noted an interaction between noise and beta diversity. At low beta diversities ordinations are more seriously affected by noise, since a greater proportion of the variation in the data is contained in random scatter caused by the sampling errors, rather than the compositional trend along the gradient. In PCA ordinations of coenoclines longer than 3HC, sequence reversals due to noise are combined with those due to involution of the extremes of the gradient, making interpretation even more problematical. Gauch, Whittaker and Wentworth (1977) considered Reciprocal Averaging (RA) to be superior to both PCA and PO in its increasing resistance to noise with increasing beta diversity.

Gauch, Whittaker and Singer (1981) found that the addition of noise generally left the basic configurations produced by Detrended Correspondence Analysis (DCA), Reciprocal Averaging (RA), Parametric Mapping and various forms of Non-metric Multidimensional Scaling (NMDS) unchanged, but introduced a degree of random scatter. If the coenocline was strongly involuted in the ordination of noiseless data, the scatter introduced by noise could intermingle samples from opposite ends of the gradient. Parametric Mapping seemed particularly vulnerable to the effects of noise. This may be due to the fact that the technique down-weights large distances, and thus becomes increasingly sensitive to noise-induced fluctuations in the smaller distances.

Recent experiments by Gauch (1982), using simulated Gaussian coenoclines, suggest that eigenvector methods (e.g. PCA, RA, DCA) tend to selectively defer noise variation to lower axes.

1.5.1.3 Sample Arrangement

Most comparative studies using data from simulated coenoclines have used samples spaced evenly along the simulated gradients. However, a few have examined the effects on ordinations of alternative sampling arrangements. Kessell and Whittaker (1976) found that PCA ordinations were adversely affected when samples were clustered in several places along a coenocline. Such a situation could arise in field sampling if some levels of a gradient were of more widespread occurrence in a landscape than others, and samples were spread fairly evenly on an areal basis. Mean displacement errors increased as much as twofold, compared to those obtained when the same coenoclines were sampled evenly. The clusters of samples tended to "attract" the principal axes.

Mohler (1981) reported a reduction in mean displacement errors on the first axes of ordinations by Detrended Correspondence Analysis (DCA) and Reciprocal Averaging (RA) when samples were concentrated towards the ends of coenoclines, rather than evenly spaced or concentrated towards the central region. In contrast, mean displacement errors in ordinations by Principal Components Analysis (PCA) showed no improvement. However, curvilinear distortion of the coenocline into the second dimension was reduced in both PCA and RA ordinations when sampling favoured the gradient extremes. On the basis of his results, Mohler recommended that field ecologists should concentrate their sampling effort at the extremes of perceived gradients. However, the logic of his approach is questionable (see section 3.5.4).

1.5.1.4 Disjunctions

Gauch, Whittaker and Wentworth studied the effect of partial disjunction on ordinations by removing two sections of adjacent samples (of lengths 1, 2 or 3HC) from a simple Gaussian coenocline with a beta diversity of 10HC. Three partially disjunct sets of samples were thus created. Polar Ordinations were unchanged except, of course, for the deletion of the missing samples. With increasing degrees of partial disjunction ordinations by Principal Components Analysis (PCA) and Reciprocal Averaging (RA) produced various types of axes differentiating between and/or within sub-sets. These were accompanied by axes representing curvilinear distortions of the underlying gradient. While neither PCA nor RA behaved particularly well in the presence of disjunctions, RA seemed to produce a greater proportion of "interpretable" axes.

Hill and Gauch (1980) examined the consequences of partial disjunction for Detrended Correspondence Analysis (DCA) using a similar procedure. DCA represented the lengths of the gaps accurately, provided they were less than about 3Z (2.2HC), and the relative positions of remaining samples on the first axis were not affected appreciably. With longer gaps, the length of the missing segment was overestimated. DCA thus appears to handle partial disjunctions much more effectively than RA.

1.5.2 Non-Gaussian Coenoclines

The study of Austin (1976a,b) used data from two simulated coenoclines with non-Gaussian species response curves, one based on arbitrary beta functions and the other incorporating competition effects and carrying capacity adjustments (section 1.2). Reciprocal Averaging (RA) did not recover the correct rank order of samples from either model. In both cases, involution of extreme samples occurred. This contrasts with the performance of RA on data from Gaussian coenoclines, where rank order recovery is always perfect in the absence of noise. However, it will be shown later (section 3.3.4) that the involution observed by Austin was a consequence of the lack of species which reach their maximum abundance at the extremes of the gradient, rather than the non-Gaussian response curves.

Parametric Mapping failed to give meaningful results with either data set. It was suspected that samples were being displaced by the technique according to differences in their totals.

Gaussian Ordination (GO) failed to converge on an acceptable solution for the beta function model. When applied to the data from the "ecological response" model, the fitted Gaussian regressions accounted for 99 percent of the total sum of squares. However, this was achieved by altering the spacing between samples and changing the rank order of one sample. It was therefore concluded that Gaussian Ordination has the capacity to "improve on nature", in order to promote the formation of Gaussian curves when the underlying model is non-Gaussian. A re-examination of Austin's "ecological response" model in the present study (section 3.3.4) showed that the sample whose rank order was

altered by GO contained only one species. The position of such samples is ambiguous for GO : they may equally well be placed on either tail of the fitted response curve for that species.

The Global Non-metric Multidimensional Scaling (GNMDS) solutions in two dimensions for both models were marred by involution. Problems with local minima prevented a unidimensional ordination of the beta function model. A unidimensional solution for the ecological response model, which appeared to be a global optimum, did recover the correct rank order of samples along the gradient. GNMDS was thus the only one of the four methods tested which produced an acceptable ordination of this model.

1.5.3 Gaussian Coenoplanes

1.5.3.1 Absolute and Relative Beta Diversities

Austin and Noy-Meir (1971) examined the effect on Principal Components Analysis (PCA) of variation in the beta diversity of the axes of two Gaussian coenoplanes. From the details given, the beta diversities of the their two models have been estimated by the present author as 6 X 7.5Z (4.4 X 5.5HC) and 4.3 X 5.3Z (3.2 X 3.9HC) respectively. On the first two axes of ordinations by unstandardised PCA, the two gradients in the models were recovered only crudely. The edges and particularly the corners of the grid were folded in towards the centre of the ordination. The involution was worse for the model with higher beta diversity. In three dimensions, the grid was distorted into a dome. Distortion was even more severe for another 6 X 7.5Z model with additional species added to the central region of the coenoplane. In this case, the second ordination axis was entirely spurious,

representing the height of the dome, and the two gradients were crudely recovered on axes one and three. Double standardisations of the data prior to PCA were sometimes effective in reducing the degree of curvature of the coenoplane and preventing the involution of extreme samples.

Gauch, Whittaker and Wentworth (1977) found that Polar Ordination (PO), Principal Components Analysis (PCA) and Reciprocal Averaging (RA) could all produce reasonable ordinations of a 1.5 X 1.5HC coenoplane. RA and PO were also successful with square coenoplanes of 4.5 X 4.5HC, reproducing the two gradients with reasonable accuracy on the first two ordination axes. However, when the coenoplane axes differed considerably in beta diversity (e.g. 4.5 X 1.5HC) the arch distortion of the longer gradient interfered with the effective recovery of the underlying structure by both PCA and RA. In such cases, the two underlying gradients were approximately recovered on axes one and three, with sample scores on the second axis bearing a roughly quadratic relationship to those on the first axis. Involution of the edges and corners of coenoplanes with moderate to high beta diversity was a problem with PCA, but not RA. PO represented the relative positions of samples more accurately when end-points were chosen at diagonally opposite corners of coenoplanes, rather than in the middle of opposite sides. This was especially so when one or both coenoplane axes were of moderate to high beta diversity (i.e. more than 3HC).

Fasham (1977) found that Global Non-metric Multidimensional Scaling (GNMDS) produced less distorted ordinations of 4.5 X 4.5HC and 4.5 X 1.5HC coenoplanes than Reciprocal Averaging (RA). However, RA

performed somewhat better than GNMDS on a 1.5 X 1.5HC coenoplane. GNMDS in two dimensions correctly recovered the two axes of the 4.5 X 1.5HC coenoplane. Working with the same models, Prentice (1980) regarded the results produced by Local Non-metric Multidimensional Scaling (LNMDS) as generally preferable to ordinations by Global Non-metric Multidimensional Scaling (GNMDS). He also recommended the use of primary, rather than secondary treatment of tied similarity values (see Appendix A, section A.6).

Gauch, Whittaker and Singer (1981) tested Detrended Correspondence Analysis (DCA), Reciprocal Averaging (RA), Parametric Mapping and various forms of Non-metric Multidimensional Scaling (NMDS) on data from simulated Gaussian coenoplanes and more complex models with up to four underlying gradients. They concluded that DCA generally produced the best ordinations. For a 4.5 X 1.5HC coenoplane, NMDS ordinations were highly arched. This contrasts with the results obtained by Fasham (1977) and Prentice (1980), both of whom obtained reasonable ordinations of 4.5 X 1.5HC coenoplanes using NMDS.

The curvilinear distortion of coenoplanes by linear ordination methods (PCA, PO, RA etc.) is simply the two-dimensional manifestation of the non-linearity problem noted with coenocline data (section 1.5.1.1). However, when there are two or more gradients, the potential interpretative difficulties caused by curvilinear distortion are even greater. It may be possible to recognise a complex curved configuration with respect to the first two or three axes of an ordination as indicative of a unidimensional trend (Feoli and Feoli Chiapella 1980). However, it is very difficult to recognise and mentally unfold a highly curved coenoplane. When one axis of a coenoplane has a higher beta

diversity than the other, curvilinear distortion of the longer gradient may hamper recognition of the secondary gradient.

1.5.3.2 Noise

The only study investigating the effects of noise on ordinations of coenoplanes appears to be that of Gauch, Whittaker and Singer (1981). Their overall conclusions have already been outlined above (section 1.5.1.2).

1.5.3.3 Sample Arrangement

Gauch, Whittaker and Wentworth (1977) examined the effect of sample clustering on ordinations by Polar Ordination (PO), Principal Components Analysis (PCA) and Reciprocal Averaging (RA) using coenoplanes of 4.5 X 1.5 and 2.5 X 1.5HC. Polar Ordinations were not affected by sample clusters, since only similarities between each sample and the end-points are considered when deriving ordination co-ordinates. RA ordinations were only slightly affected, while PCA ordinations showed slight to extensive deterioration. The principal axes were attracted by sample clusters (cf. Kessell and Whittaker 1976). When the clusters were not at the edges of the coenoplane, spurious axes could result, with representation of the coenoplane being increasingly distorted.

These preliminary experiments suggest that the effect of non-regular sampling arrangements on the ordination of coenoplanes merits further study (see also section 1.5.1.3).

1.5.3.4 Outliers

Gauch, Whittaker and Wentworth (1977) created artificial outliers or deviant samples of two kinds. Type "a" outliers were produced by random selection, for each species, of one of its abundances from among the samples comprising the data set. Type "b" outliers were created by allocating a high abundance to one randomly selected species, then giving about half the remaining species random but moderate abundances, and half zeroes. Outliers of type "a" were meant to simulate moderately deviant samples from atypical habitats, while those of type "b" were thought to approximate strongly deviant samples from disturbed sites. The effect on ordinations of adding one,three or five outliers to data sets from simulated coenoclines and coenoplanes was examined.

Unless chosen as reference samples, outliers had no effect on Polar Ordination, both types appearing near the centre of the ordination. Reciprocal Averaging (RA) was robust to type "a" outliers, whereas type "b" outliers had unpredictable but potentially severe effects. Type "b" outliers were generally isolated on the first or second RA axis, and the recovery of the underlying gradients within the remaining samples was distorted. One type "a" outlier generally had little effect on Principal Components Analysis (PCA) ordinations, but three or five caused some displacement of the other samples. Type "b" outliers had severe effects on PCA.

1.6 Conclusions Regarding Individual Methods

1.6.1 Polar Ordination

The simulation studies which have examined Polar Ordination (PO) (Gauch and Whittaker 1972b; Kessell and Whittaker 1976; Gauch, Whittaker and Wentworth 1977) have all used samples known to represent the extremes of simulated gradients as ordination poles. Gauch and Whittaker (1972b) noted that this may seem to bias the comparison in favour of PO, but claimed that the choice of samples representing the extremes of environmental gradients was normal practice in the application of PO to field data. Such a procedure assumes prior knowledge by the ecologist of the major underlying gradients and their extremes. PO cannot therefore be regarded as a strictly indirect ordination technique. While it may be true that users of PO endeavour to choose samples respresenting the extremes of environmental gradients, there is no guarantee that their choices are always successful. Automatic criteria for the selection of end-points are generally ineffective (Gauch 1973b; Gauch, Whittaker and Wentworth 1977), especially in the presence of outlier or deviant samples or when beta diversity is high. Gauch (1973b) suggests the use of composite-samples (i.e. averages of several individual samples) as ordination poles, since averaging tends to reduce the effects of sampling errors and other irregularities influencing the composition of individual end-point samples (cf. Kirkpatrick and Hutchinson 1977).

Provided that the chosen reference samples do represent the extremes of the underlying gradients, PO is capable of producing effective ordinations of coenoclines and coenoplanes with beta

diversities up to about 3HC (Gauch 1973b). The anchoring of the extremes of the gradient by the reference stands prevents the involution of extreme samples when distance measures such as percentage difference (PD) or its binary equivalent (CD) are used, but involution can occur with Euclidean distance. Since sample positions are determined solely by their relationships to the reference samples, PO is unaffected by sample clustering and outliers, provided the latter are not chosen as end-points (Gauch, Whittaker and Wentworth 1977).

1.6.2 Principal Components Analysis

Of the ordination techniques in widespread use in plant ecology, Principal Components Analysis (PCA) in its most familiar form (unstandardised, centred by species) appears to be the most vulnerable to curvilinear distortion of underlying gradients with increasing beta diversity. Curvilinear distortion of coenoclines, with consequent involution of extreme samples on the first ordination axis is a serious problem above about 3HC (4Z). Analogous problems occur with coenoplanes. Standardisation by species or double standardisation may decrease distortion in some cases (Austin and Noy-Meir 1971; Gauch, Whittaker and Wentworth 1977) and extend the range of beta diversity which can be ordinated without involution.

PCA is also strongly affected by sample clusters and outliers, and it appears more sensitive to sampling errors than Polar Ordination (using the PD measure) and Reciprocal Averaging (Kessell and Whittaker 1976; Gauch, Whittaker and Wentworth 1977).

These results suggest caution in the application of PCA to

vegetation data for the purpose of indirect gradient analysis. The interpretation of PCA ordinations should take full account of the possibility of curvilinear distortion of underlying gradients. Best results will be obtained with PCA when the beta diversities of all underlying gradients are less than about 3HC (4Z).

1.6.3 Reciprocal Averaging

Like PCA, Reciprocal Averaging (RA) is subject to curvilinear distortion of underlying gradients when beta diversity is moderate to high. However, the simultaneous double standardisation implicit in RA (see Appendix A, section A.4) prevents involution of the gradient extremes, even at very high beta diversities (Gauch, Whittaker and Wentworth 1977).

RA produces effective ordinations of coenoplanes when the beta diversities of the axes are approximately equal. However, when one coenoplane axis is considerably longer than the other, the second ordination axis reflects a spurious arch distortion of the primary gradient and the secondary gradient may appear on the third RA axis (Fasham 1977; Gauch, Whittaker and Wentworth 1977). The results of Gauch, Whittaker and Wentworth (1977) show that RA is relatively resistant to the effects of sample clusters and noise, but is badly affected by outliers.

1.6.4 Detrended Correspondence Analysis

Detrended Correspondence Analysis (DCA) represents a deliberate attempt to overcome some of the limitations of Reciprocal Averaging (Hill and Gauch 1980). The detrending process used in DCA reduces the eigenvalues of curvilinear distortion axes. DCA ordinations of coenoplanes in which one gradient has a considerably higher beta diversity than the other, correctly recover the two gradients on axes one and two, while further, spurious axes have very low eigenvalues (Hill and Gauch 1980; Gauch, Whittaker and Singer 1981). However, detrending does not eliminate problems with spurious distortion axes completely. Although the second and subsequent axes are individually detrended with respect to each previously extracted axis, it is possible for systematic relationships to remain with respect to interactions of the previous axes (Hill and Gauch 1980). The rescaling procedure incorporated into DCA appears to improve the accuracy with which the method recovers the positions of samples along artificial Gaussian coenoclines (Gauch, Whittaker and Singer 1981; Mohler 1981).

Gauch, Whittaker and Singer (1981) regarded DCA ordinations of artificial data from models with up to four underlying gradients to be generally superior to those produced by Reciprocal Averaging, Parametric Mapping and various forms of Non-metric Multidimensional Scaling. They considered DCA to be the best currently available method for indirect gradient analysis. However, the present study does not support this conclusion (see Chapters 2-5).

1.6.5 Non-metric Multidimensional Scaling

Fasham (1977) found that ordinations of simulated coenoclines and coenoplanes by Global Non-metric Multidimensional Scaling (GNMDS) were generally superior to those produced by Reciprocal Averaging (RA), and always better than Principal Components Analysis (PCA) solutions. The correct rank order of samples along coenoclines was always recovered when one dimension was specified for NMDS ordinations. However, when two dimensions were allowed, the coenocline was curved into the second dimension and involution of exreme samples on the first axis could occur. Specification of the correct dimensionality thus appears to be important. Ordinations of coenoplanes by GNMDS were superior to those produced by RA, especially when the coenoplane axes differed in beta diversity.

Prentice (1977,1980) found that the local form of Non-metric Multidimensional Scaling (LNMDS) generally produced better ordinations than the global form, but expressed doubt as to whether NMDS should be recommended in preference to Reciprocal Averaging in view of the much greater computational load involved in NMDS. However, GNMDS was the only one of the methods tested by Austin (1976b) which correctly recovered the rank order of samples for his ecological response model. Gauch, Whittaker and Singer (1981) considered that both DCA and RA performed better than both global and local NMDS with data from simulated Gaussian coenoclines. For models with two or more gradients, NMDS gave better results than RA provided that the correct dimensionality was specified, but DCA ordinations seemed generally preferable.

The position of NMDS as a method of ecological ordination is equivocal. Further work is required before it can be clearly established whether the computational and other difficulties involved in NMDS (see Appendix A, section A.6) are outweighed by the quality of its solutions.

1.6.6 Parametric Mapping

Noy-Meir (1974a) used Parametric Mapping on data from a simple simulated coenocline. Given one dimension, Parametric Mapping recovered the original order and spacing of the samples well, but when two dimensions were allowed, the coenocline appeared highly arched in the ordination. Analogous problems occurred with a simple Gaussian coenoplane. Austin (1976b) reported that Parametric Mapping failed to produce reasonable ordinations of data from two non-Gaussian coenoclines. He suspected that samples were being displaced by the method according to differences in their totals. Gauch, Whittaker and Singer (1981) reported problems with local minima, especially with unidimensional solutions. They also found that Parametric Mapping had a tendency to isolate a few points. As a minimum was approached, the size of the step through which points are moved each iteration is reduced and some points seemed to lag behind. In addition, the method appeared to be highly sensitive to noise.

Other practical difficulties which limit the effectiveness of Parametric Mapping include unexplained failures of the algorithm with large data sets and some parameter settings (Noy-Meir 1974a), uncertainty about the choice of values for the power parameters used in the non-continuity index, and the lack of a consistent relationship

between the final value of the index and the quality of the solution (Noy-Meir and Whittaker 1977). Some of the problems are probably related to the minimisation algorithm used in the program PARAMAP, although more fundamental shortcomings concerning the form of the non-continuity index have been suggested (Kruskal and Carroll 1969).

Despite its theoretical appeal and promising results with simple data sets, Parametric Mapping would appear to have limited potential as an ordination method in plant ecology.

1.6.7 Gaussian Ordination

The model assumed by Gaussian Ordination is highly specific : species abundance profiles along a single underlying gradient are Gaussian in form. With noiseless data from simulated Gaussian coenoclines, the method achieves very accurate recovery of sample positions (Gauch, Chase and Whittaker 1974). However, when beta diversity and/or sampling error is high, a reasonable starting configuration is required. Gauch, Whittaker and Singer (1981) found that Gaussian Ordination could achieve greater accuracy in the recovery of sample positions along a simulated 5HC coenocline than DCA, RA or NMDS, although they considered that the superiority of Gaussian Ordination over DCA in this respect was unlikely to be significant with noisy field data.

Austin (1976b) noted that Gaussian Ordination is inappropriate for data sets with more than one underlying gradient. When applied to data from a simple Gaussian coenoplane the method failed to recover one of the principal diagonals of the coenoplane as a best unidimensional

representation. More significantly, he found that Gaussian Ordinations were unsuccessful when applied to data from coenoclines with non-Gaussian species response curves. The effect of variation in the form of species response profiles on the performance of Gaussian Ordination requires further study.

The usefulness of Gaussian Ordination, and other methods which assume a specific form of relationship between species abundances and underlying gradients, may be limited. Orloci (1979) notes that the potential problems arising from the use of an inappropriate non-linear model for ecological ordination may be just as severe as those resulting from the application of linear ordination methods to non-linear data structures.

1.7 Conclusion

The use of artificial data, from simplified vegetation-gradient models, has proven to be a valuable approach to the comparative evaluation of ordination methods for the purpose of indirect gradient analysis. The ability to control various properties of artificial data sets (e.g. beta diversity, noise, sampling arrangements) has facilitated an increased understanding of their effects on ordination performance, both alone and in combination. The clear recognition of the problems caused by the intrinsic non-linearity of vegetation data for the interpretation of linear ordinations is largely attributable to the insights provided by the simulation approach.

However, nearly all the simulation studies have been based on models in which the response curves or surfaces were assumed to be of

Gaussian form. The preliminary experiments of Austin (1976a,b) suggest that even the most promising of recently introduced ordination techniques may be undesirably sensitive to departures from the Gaussian model. Since observational evidence in favour of the universal applicability of the Gaussian model in nature is lacking (Austin 1980; van der Maarel 1980; Werger, Louppen and Eppink 1983), the significance of the detailed conclusions of simulation studies using Gaussian models is in doubt. Greig-Smith (1980) writes :

> "The alternative of testing methods on simulated data has little relevance until we know how to simulate realistic data."

In future simulation studies, efforts should be made to develop vegetation-gradient models which encompass the full richness of concepts arising from the results of suitably designed direct gradient analyses and experimental studies. The present work is intended as a first step in this direction.

CHAPTER 2 : SIMULATION AND ASSESSMENT METHODS

2.1 Vegetation-Gradient Models

2.1.1 Introduction

The present study compares the performance of a range of ordination techniques, using simulated data from both one- and two-dimensional vegetation-gradient models. A flexible modelling approach was developed, which attempts to encompass the diversity of current concepts concerning vegetation-gradient relationships. These concepts have been developed from a consideration of the results of direct gradient analyses (including the analysis of the vegetation of the Mt. Field Plateau, reported in Chapter 8 of this thesis) and experimental gradient studies (Ellenberg 1953,1954; Mueller-Dombois and Sims 1966; Mueller-Dombois and Ellenberg 1974; Austin and Austin 1980). The available evidence appears insufficient to permit a general model of vegetational response to environmental gradients to be formulated (cf. Austin 1980). Hence a major aim of the present study was to identify ordination techniques which are robust to plausible variations in those features of a vegetation-gradient model which are still subject to debate (especially the form of response curves). The view was taken that an ordination method which performs well on a range of plausible models is most worthy of the interim reliance of ecologists, as a "general purpose" method for indirect gradient analysis.

The modelling approach used in the present study represents, in part, a merger of some features of the Gaussian models of Whittaker and Gauch (1972a, 1976) and the beta function and "ecological response" models of Austin (1976a), together with several extensions and some

novel characteristics. A suite of computer programs for coenocline and coenoplane simulation was developed for use in the present study. The various features and options incorporated into these programs will now be described.

2.1.2 Physiological Response Curves

In the absence of interference from other species, the abundance profile of a species along an environmental gradient (i.e. its "physiological" response curve) was assumed to be unimodal in form, though not necessarily symmetrical. In order to simulate physiological response curves, a function was required which is capable of producing unimodal curves of varying skewness. The function chosen was the beta function (equation 4), first suggested for this purpose by Austin (1976a). In the present case, interest centres on the behaviour of the function when values of X range from zero to unity and both powers α and γ are positive. Under these conditions, the curve described by the beta function is unimodal and its degree of skewness may be altered by varying the relative values of the powers α and γ. When α and γ are equal, symmetrical curves are produced. Skewed curves can be obtained by using unequal powers.

In order to be useful for a vegetation-gradient model, it must be possible to specify the height of the curve at its mode, the position of the mode along a coenocline and the range of the curve (i.e. the length of that portion of the coenocline axis over which the species abundance is non-zero). In the form given in equation 4, the maximum value of the function occurs at $X=\alpha/(\alpha+\gamma)$ and the value of the function there is

$$\frac{\alpha^{\alpha} \cdot \gamma^{\gamma}}{(\alpha+\gamma)^{(\alpha+\gamma)}}$$

which shall be designated here as the constant C1. Control of the height of the curve at its mode is achieved by multiplying the function by A0/C1, where A0 is the required abundance at the mode. Suppose that one requires the mode to be located at X=M and the range of the species along the coenocline to be R. In that case, the lower limit of the species distribution along the coenocline, X0, is given by $X0=M-R.\alpha/(\alpha+\gamma)$. In order to adjust the range of the beta function, the argument, X, is replaced by (X-X0)/R, this expression having the required range of zero to unity.

The abundance, A at a point X on the coenocline is then given by

$$A = \begin{cases} 0 & X < X0 \\ \frac{A0}{C1}\left(\frac{X-X0}{R}\right)^{\alpha}\left(1 - \frac{X-X0}{R}\right)^{\gamma} & X0 \leqslant X \leqslant X0+R \\ 0 & X > X0+R \end{cases} \qquad (5)$$

where A0 is the abundance of the species at its mode, C1 is the constant defined above (which depends only the values of α and γ), R is the range of the species along the coenocline, α and γ are positive constants controlling the skewness of the curve and X0 is the lower limit of the species on the coenocline. An alternative formulation, which includes the location of the mode, M, rather than X0 is as follows :

$$A = \begin{cases} 0 & X < XO \\ \dfrac{AO}{C1}\left(\dfrac{X-M}{R} + C2\right)^{\alpha}\left(\dfrac{M-X}{R} + C3\right)^{\gamma} & XO \leqslant X \leqslant XO+R \\ 0 & X > XO+R \end{cases} \qquad (6)$$

where C2 and C3 are constants defined as $C2=\alpha/(\alpha+\gamma)$, $C3=\gamma/(\alpha+\gamma)$. Some examples of the types of response curves which can be produced by this flexible beta function are given in Figure 2.1.

The models of Gauch and Whittaker (1972a, 1976) make no provision for the fact that the probability of occurrence of a species may also vary systematically along an environmental gradient, in addition to its mean abundance (Austin and Cunningham 1981; Goodall and Johnson 1982; Austin, Cunningham and Good 1983; see also Chapter 8). In the present programs, it is assumed that the response curve for probability of occurrence of a species has the same range (R) and modal position (M) as the abundance curve, but a "broader" shape, with less rapidly descending flanks on either side of the mode. This broader shape is achieved by using powers α and γ each equal to one half of the corresponding values used for the abundance curve. The probabilities of occurrence at the mode (PO) are separately allocated.

The probability of occurrence, P, at a point X on the gradient is thus given by

$$P = \begin{cases} 0 & X < XO \\ \dfrac{PO}{C1}\left(\dfrac{X-XO}{R}\right)^{\alpha/2}\left(1 - \dfrac{X-XO}{R}\right)^{\gamma/2} & XO \leqslant X \leqslant XO+R \\ 0 & X > XO+R \end{cases} \qquad (7)$$

where C1 is the same constant which appears in equation (5) above. The probability profiles are only used if it is desired to introduce

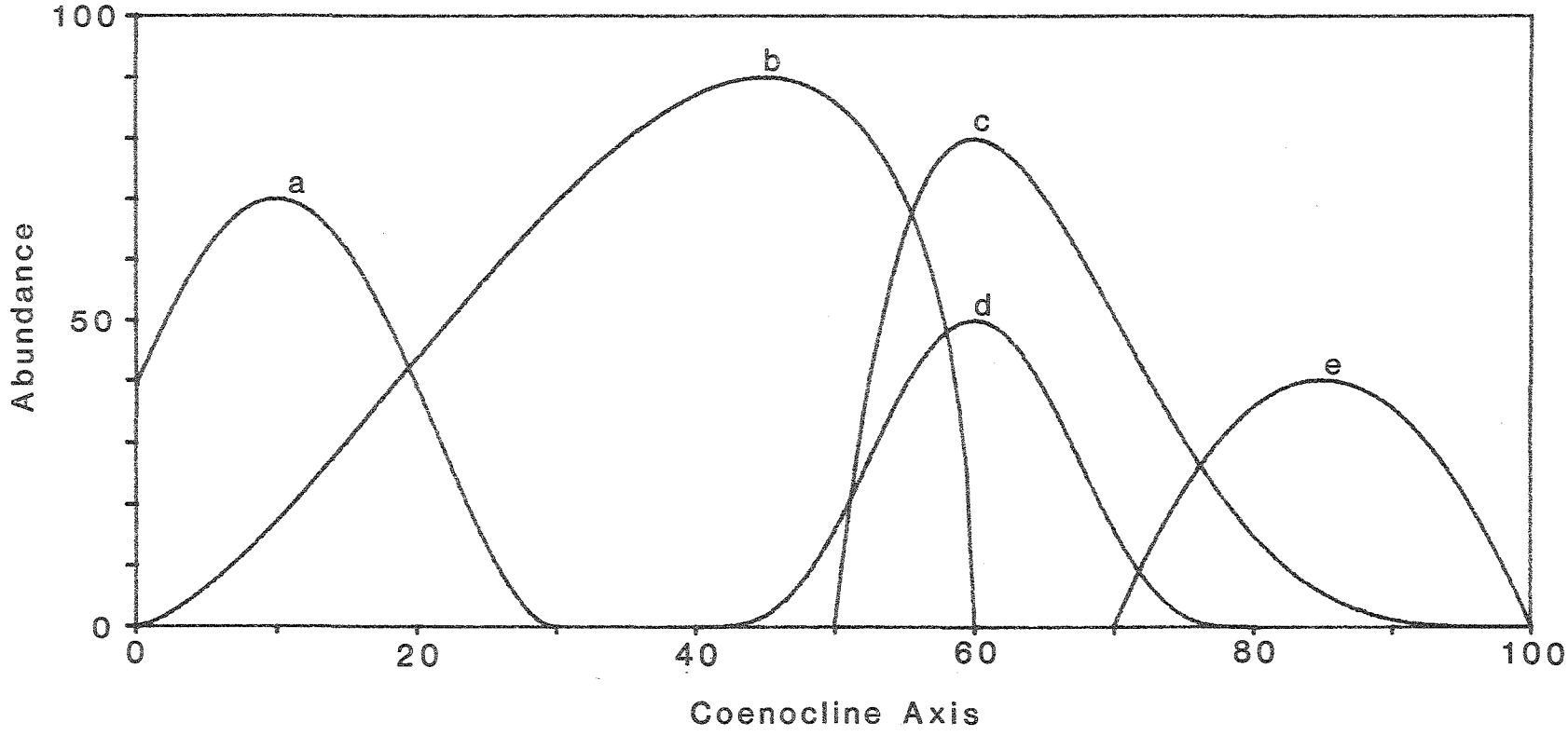


Figure 2.1 Some examples of the types of species response curves which may be produced using the flexible beta function. Parameters of the five curves illustrated are as follows: (a) A0=70, 0=10, R=40, $\alpha=\gamma=2$; (b) A0=90, 0=45, R=60, $\alpha=1.5$, $\gamma=0.5$; (c) A0=80, 0=60, R=50, $\alpha=1$, $\gamma=4$; (d) A0=50, 0=60, R=40, $\alpha=\gamma=4$; (e) a0=40, 0=85, R=30, $\alpha=\gamma=1$.

qualitative "noise" into the data. This will be explained in detail later (section 2.1.5.2).

In order to facilitate the simulation of coenoplanes, the beta function was generalised to produce unimodal, though possibly skewed, response surfaces in two dimensions. Suppose that a particular species has its mode located at the point (Mx,My) in the plane defined by X and Y axes representing a pair of environmental gradients, and that its abundance at the mode is A0. Let the ranges of the species along the X and Y axes be Rx and Ry respectively. The abundance, A, of the species at a point (X,Y) on the coenoplane is then given by

$$A = \begin{cases} 0 & X < X0 \text{ or } Y < Y0 \\ \dfrac{A0}{C1}\left(\dfrac{X-X0}{Rx}\right)^{\alpha x}\left(1-\dfrac{X-X0}{Rx}\right)^{\gamma x}\left(\dfrac{Y-Y0}{Ry}\right)^{\alpha y}\left(1-\dfrac{Y-Y0}{Ry}\right)^{\gamma y} & \begin{array}{r} X0 \leq X \leq X0+Rx \\ \text{and } Y0 \leq Y \leq Y0+Ry \end{array} \\ 0 & X > X0+Rx \text{ or } Y > Y0+Ry \end{cases} \quad (8)$$

where αx and γx are positive constants controlling the skewness of the surface with respect to the X axis, αy and γy are positive constants controlling the skewness of the surface with respect to the Y axis, X0 (the lower limit of the species on the X axis) is equal to $Mx-Rx.\alpha x/(\alpha x+\gamma x)$, Y0 (the lower limit of the species on the Y axis) is equal to $My-Ry.\alpha y/(\alpha y+\gamma y)$ and C1 is a constant equal to

$$\frac{\alpha x^{\alpha x}\,.\,\gamma x^{\gamma x}}{(\alpha x+\gamma x)^{(\alpha x+\gamma x)}} \cdot \frac{\alpha y^{\alpha y}\,.\,\gamma y^{\gamma y}}{(\alpha y+\gamma y)^{(\alpha y+\gamma y)}}$$

An alternative formulation, analogous to equation (6), involving the location of the mode (Mx,My) rather than the lower limits (X0,Y0) is possible, but will not be given here. Contour diagrams illustrating

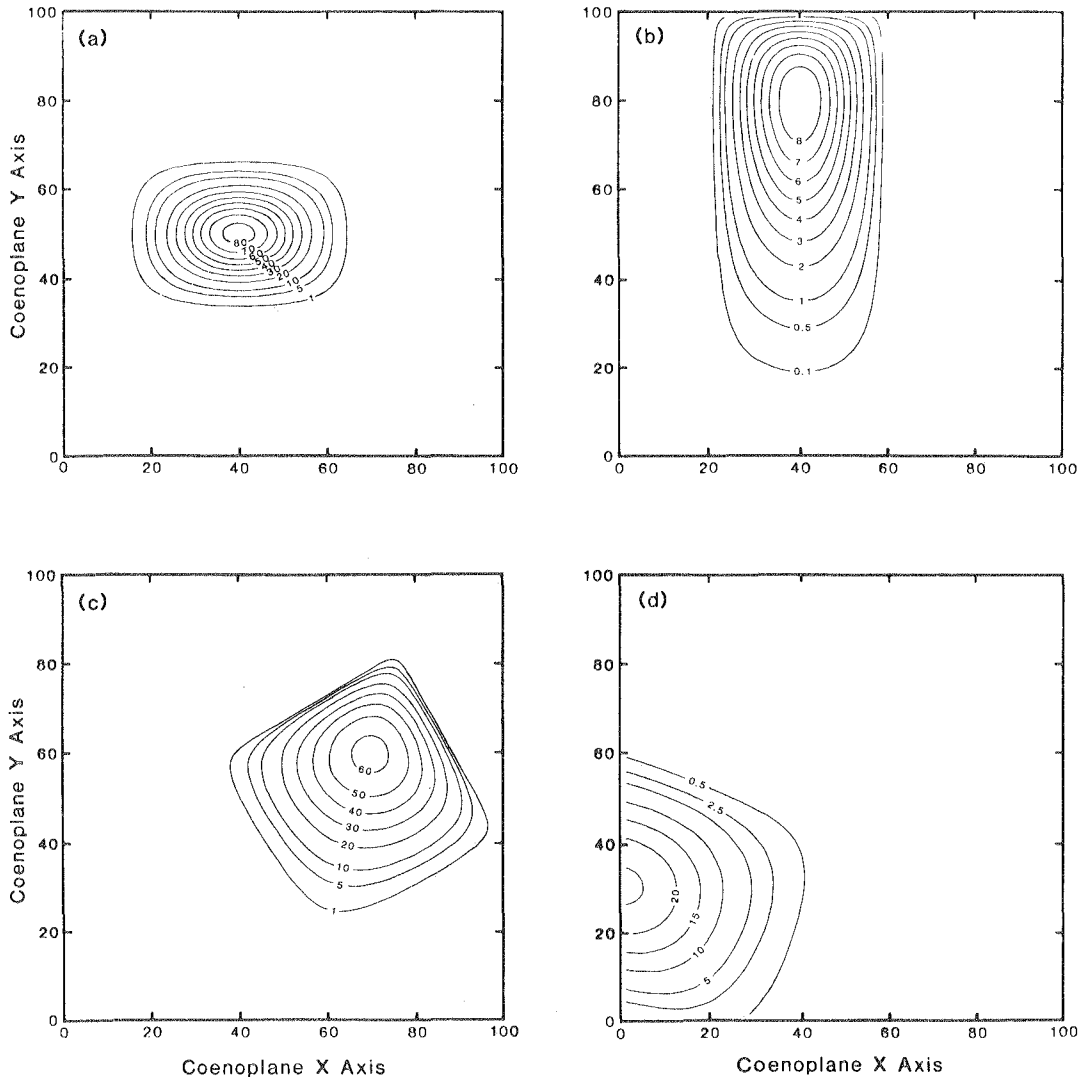


Figure 2.2 Some examples of the types of species response surfaces which may be produced using the two-dimensional generalisation of the flexible beta function. Contours in these diagrams join points on the response surfaces of equal species abundance. Parameters of the four surfaces illustrated are as follows: (a) A0=85, 0x=40, 0y=50, Rx=60, Ry=40, $\alpha x=\gamma x=\alpha y=\gamma y=4$, $\theta=0^{o}$; (b) A0=9, 0x=40, 0y=80, Rx=40, Ry=100, $\alpha x=\gamma x=2$, $\alpha y=4$, $\gamma y=1$, $\theta=0^{o}$; (c) A0=63, 0x=70, 0y=60, Rx=50, Ry=50, $\alpha x=\alpha y=2$, $\gamma x=\gamma y=1$, $\theta=30^{o}$; (d) A0=26, 0x=0, 0y=30, Rx=100, Ry=60, $\alpha x=\gamma x=4$, $\alpha y=\gamma y=2$, $\theta=-20^{o}$.

some of the types of response surfaces which can be produced using the two-dimensional beta function are given in Figure 2.2.

Gauch and Whittaker (1976) included an option in their coenocline simulation program which allowed the Gaussian response surface of a species to be rotated through an angle θ with respect to the X axis of the coenoplane. A similar facility was included in the present program. Rotation of the response surface is achieved by replacing the original arguments X and Y in equation (8) above by transformed values, X' and Y', defined by

$$X' = Mx + (X-Mx)\cos\theta + (Y-My)\sin\theta \qquad (9)$$

$$Y' = My + (Y-My)\cos\theta - (X-Mx)\sin\theta \qquad (10)$$

where θ is the required angle of rotation with respect to the X axis of coenoplane.

Two-dimensional probability of occurrence surfaces are defined in a manner analogous to the probability profiles used for coenoclines : the probability surface for a species is given the same modal position (Mx,My) as the abundance surface and the same ranges in the X and Y directions (Rx,Ry), but powers αx, γx, αy and γy are set at one half their corresponding values for the abundance surface. The probability of occurrence (P) at a point (X,Y) on the coenoplane is thus given by

$$P = \begin{cases} 0 & X < X0 \text{ or } Y < Y0 \\ \dfrac{P0}{C1}\left(\dfrac{X-X0}{Rx}\right)^{\alpha x/2}\left(1-\dfrac{X-X0}{Rx}\right)^{\gamma x/2}\left(\dfrac{Y-Y0}{Ry}\right)^{\alpha y/2}\left(1-\dfrac{Y-Y0}{Ry}\right)^{\gamma y/2} & X0 \leq X \leq X0+Rx \text{ and } Y0 \leq Y \leq Y0+Ry \\ 0 & X > X0+Rx \text{ or } Y > Y0+Ry \end{cases} \qquad (11)$$

where P0 is the probability of occurrence at the mode and the other

symbols have the same meanings as in equation (8).

2.1.3 Allocation of Species Response Parameters

In the unidimensional case, the abundance profile (equation 5) of each species is defined by five parameters. These are : the location of the mode (M), the maximum abundance of the species at its mode (A0), the range of the coenocline over which the species occurs (R), and the powers α and γ, which control the skewness of the response curve. In all models, the length of the sampled region of the simulated coenoclines is set at 100 arbitrary units. The average magnitude of the distributional ranges (R) of the species occurring in a coenocline controls the beta diversity, or degree of compositional change, along the coenocline. An input parameter, Z, is used to regulate beta diversity in a manner analogous to that adopted by Gauch and Whittaker (1972a) for their Gaussian models. In order to make the beta diversities produced by a given value of Z in the present models more or less comparable to those in the Gaussian models, it was assumed that the effective "range" of a Gaussian distribution is equal to about six standard deviations. The average species range, Rbar, is thus computed as 600/Z in the present programs. In other words, Z is a measure of the length of the coenocline in units of 1/6 average species ranges (cf. Gauch and Whittaker 1972a). Values of R for individual species are selected randomly from a normal distribution with a mean of Rbar and a standard deviation equal to S.Rbar, where S is a user-supplied parameter analogous to the STD of Gauch and Whittaker (1972a). The default (standard) value of S is 0.3.

Gauch and Whittaker (1972a) selected response curve maxima

randomly from either a lograndom distribution on the range 0.01 to 100 or a lognormal distribution with user-supplied parameters. A similar approach is used in the present models to allocate values of A0, with the additional flexibility that the lower limit for a lograndom distribution may be set to any positive value.

Values for the power α are randomly assigned for each species from a uniform distribution with user-supplied minimum and maximum. If a constant value is required for all species, these limits are simply set equal. A similar procedure is used to allocate values for the other power, γ. An additional option allows the value of γ for each species to be set equal to the previously allocated value of α, thus ensuring that all curves are symmetrical.

For the purpose of allocating the positions of species modes (M), the coenocline axis is extended at each end by an amount equal to 2/3 of the average species range, Rbar. A similar procedure was adopted by Gauch and Whittaker (1972a), to avoid "edge-effects" and place the central, sampled region of the gradient (0 to 100) within a uniform compositional gradient. Failure to place any species with modes outside each end of the coenocline would result in a lack of monotonic curve "tails", extending into the sampled region from each end. The extended coenocline axis ranges from -2Rbar/3 to 100+2Rbar/3. Initially, the mode (M) of each species is placed randomly within this range. The positions of the modes of "major" species may then be adjusted so that they are distributed more uniformly along the gradient (cf. Gauch and Whittaker 1972a). Major species are defined as those M% of the species in the model with the highest abundance curve integrals, where M is a user-specified constant, with a default value of 15%. Curve integrals

are computed approximately using numerical integration. Major species are assigned segments of the coenocline in proportion to their integrals and the mode of each major species is then moved to the centre of its segment. The program of Gauch and Whittaker (1972a) performs such adjustments routinely, but it was considered more expedient in the present case to make them optional. The process of selecting and flagging "major" species is performed whether or not readjustment has been selected, since the concept of major species is also used for some other purposes in the simulations (see below).

In order to allow the alpha diversity (number of species per sample) to be varied along the gradient, the present programs allow the coenocline to be divided into a user-specified number of segments of equal length. The relative numbers of species modes to be placed in each segment can then be specified. Within each segment, the positions of the modes of minor and major species are allocated in the manner described for the entire gradient : the modes of minor species are randomly scattered, while those of major species may be optionally readjusted to a more uniform distribution.

Probability of occurrence profiles (equation 7) are defined for each species, using the same modal position (M) and range (R) as the abundance profile and values of α and γ one half those used for the abundance profile. The assignment of values for probability of occurrence at the mode (P0) is performed randomly from a specified frequency distribution. Examination of the probability of occurrence profiles of species along altitudinal and drainage gradients on the Mt. Field Plateau, Tasmania (see Chapter 8 of this thesis) suggested a

Probability profile maximum (P_o) Class Limits	Relative Frequency
0.2 - 0.4	0.167
0.4 - 0.6	0.222
0.6 - 0.8	0.278
0.8 - 1.0	0.333

Table 2.1 The default frequency distribution used to allocate probability profile maxima to species in the simulations.

frequency distribution for PO of the type shown in Table 2.1. This distribution was used as a default in the simulation programs, although an alternative frequency distribution may be be specified if desired. Species flagged as "major" (as defined above) are all allocated PO values randomly on the range 0.8 to 1.0, since the Mt. Field data suggested that species with the greatest modal abundances also had probability maxima in excess of 0.8.

Allocation of the parameters for two-dimensional species abundance surfaces (equation 8), for use in simulated coenoplanes, follows the same basic principles as in the unidimensional case. In common with Gauch and Whittaker (1976), the X axis parameters for a given species ($Mx, Rx, \alpha x, \gamma x$) are assumed to be uncorrelated with those for the Y axis. Four options are allowed for the allocation of rotation angles, θ (see equations 9,10). These allow :

(1) all angles to be set to zero,

(2) all angles to be set to some constant value,

(3) angles to be allocated randomly from a uniform distribution between user-specified limits or

(4) angles to be allocated from a normal distribution with user-specified mean and standard deviation.

In allocating the positions of species modes, both the X and Y axes of the coenoplane may be optionally divided into specified numbers of segments. The relative numbers of species whose modes are to be placed in each resulting cell of the coenoplane can then be specified. This device allows alpha diversity to be varied across the coenoplane in a flexible manner.

2.1.4 Location of Samples

Three options are allowed for arrangement of samples along simulated coenoclines. These are :

(1) uniform distribution, with samples equally spaced along the entire length of the gradient (from 0 to 100),

(2) random distribution, with sample positions selected randomly between 0 and 100 and

(3) purposive, with the position of each sample being specified by the user.

Any of these options may be exercised simultaneously. For example, one may place 20 samples uniformly along the coenocline and then add another 5 samples in random positions.

Additional flexibility is achieved by allowing the coenocline to be divided into a specified number of segments of equal length. The relative numbers of samples to be placed regularly and/or randomly within each segment may then be specified. This allows uneven or clumped sampling patterns to be produced.

Similar sampling options are available for coenoplanes. Samples may be placed :

(1) on a regular grid,

(2) at random over the coenoplane or

(3) at user-specified points on the coenoplane.

Coenoplanes may be divided into cells by segmenting X and/or Y axes, and the relative numbers of samples to be placed uniformly or randomly within each cell may then be specified.

2.1.5 Generation of Data

Given the parameters defining the physiological response curves (or surfaces) of I species, and the positions of J samples on a coenocline or coenoplane, an I X J data matrix can be produced using equation (5) or (8) respectively. Optionally, this primary or "physiological" data matrix may then be modified, in order to simulate the effects of interspecific competition, qualitative (presence-absence) noise (as represented by the probability of occurrence profiles or surfaces), limitation of the total abundance of all species in a sample by an environmental "carrying capacity" and quantitative sampling errors or noise. The order of discussion of each of these processes reflects the order in which they are (optionally) applied in the simulation programs.

2.1.5.1 Competition

The approach used to introduce "competition" between species is similar to that suggested by Austin (1976a; see also Fresco 1982). For each pair of species (i and j, say) a linear interaction coefficient Cij is defined, which expresses the degree to which the abundance of species j in a sample reduces the abundance of species i. The method of assigning values for the Cij coefficients will be described later. Suppose that the abundance of species i in a sample, k, in the "physiological" data matrix is represented by Aik. This abundance is reduced by an amount equal to $\Sigma Cij.Ajk$, where Ajk is the abundance of species j in sample k and the summation extends over all species represented in the data, with the exception of species i. If the resulting value of Aik is less than zero, it is replaced by zero.

In initial versions of the programs, the interaction coefficients, Cij, were allocated randomly on the range 0 to Cmax, where Cmax is a user-specified value, less than unity. Two undesirable consequences were noted. Firstly, species with low modal abundances (AO) were nearly all reduced to "extinction" by competition, even at relatively low values of Cmax. Secondly, the "tails" of the curves of most species were severely truncated. Several modifications to the procedure for allocating the interaction coefficients were therefore introduced.

Firstly, the potential degree of competition between two species was assumed to decrease linearly with increasing distance between their modes, reaching zero for a pair species whose modes are further apart than one half of the average species range. Thus Cmax would only be used as the upper limit for random allocation of Cij values for a pair species with coincident modes. With increasing distance between modes, the upper limit declines linearly, reaching zero when the distance is greater than or equal to Rbar/2.

Secondly, where the modal abundance of species i (AOi) is less than the modal abundance of species j (AOj), the allocated value of the interaction coefficient Cij (which expresses the competitive effect of species j on i) is multiplied by the ratio AOi/AOj.

Finally, the total amount of competition allowed against any given species, i, is controlled as follows :

(1) Estimated "maximum competitive decrements" against species i, due to each jth species, are computed as Cij.AOj, and a running total of these values is kept as the Cij coefficients are allocated for

each jth species in a random order.

(2) When this running total exceeds Clim.AOi, where Clim is a user-specified positive constant less than unity, the Cij values for all remaining species, j, against species i are set to zero.

The justification for these procedures is purely empirical : they tend to produce shouldered, bimodal and multimodal "ecological response curves", similar in form to those often observed in direct gradient analyses. Accurate simulation of the underlying mechanisms involved in the modification of physiological response profiles by interspecific competition along an environmental gradient is not claimed.

2.1.5.2 Qualitative (Presence-absence) Noise

If desired, qualitative noise can be introduced into the data using the probability of occurrence of each species in a given sample, as computed using equation (7) or (11). For each species occurring in the sample, a random number is selected from a uniform distribution on the range zero to unity. If this value exceeds the computed probability of occurrence, the abundance value for that species is replaced by zero.

2.1.5.3 Carrying Capacity Adjustments

Optionally, the abundance values of all species occurring in a given sample may be adjusted, in order that the total of the abundances within a sample (=stand abundance of Austin 1981) has some specified relationship to the simulated gradient(s). Stand abundance may be regarded as a reflection of the "environmental carrying capacity" at the position on the gradient(s) occupied by the sample. Two options are available in the current programs :

(1) The sample totals are equalised over the entire coenocline or coenoplane. The total of each sample is first computed and the average of these totals, Sbar, is obtained. Abundance values for species within each sample are then adjusted so that each sample has a total of Sbar. This is achieved by multiplying each value in a sample by Sbar/S, where S is the sample total before adjustment.

(2) A table is supplied specifying, for selected points on the coenocline or coenoplane, the relative sample total (as a proportion of Sbar) required at that point. In the case of coenoclines, sample totals are then computed for each existing sample using simple linear interpolation between these points. For example, if the relative total is specified as being 0.7 at X=50 and 0.9 at X=70, a sample located at X=60 would be assigned a total of 0.8Sbar. In the case of coenoplanes, the required total for a sample is computed as a weighted mean of the values specified at the four nearest points, the weights being inversely related to the distances between the sample and each of the points. More elaborate multidimensional interpolation procedures are possible, but were not considered necessary here.

After sample totals have been adjusted, it is possible that the abundance values for some species in some samples may exceed 100. Should this occur, all values in the data matrix are proportionally reduced so that the maximum value in the matrix is 100.

2.1.5.4 Quantitative Sampling Errors or Noise

Quantitative sampling errors or "noise" were introduced using the same method as Gauch and Whittaker (1972a). The procedure assumes that sampling errors are normally distributed, with a mean of zero and a standard deviation equal to $F.\sqrt{Aij(100-Aij)}$, where F is a user-specified value and Aij is the abundance of species i in sample j. Thus abundance values around 50 are subject to greater sampling errors than both high and low values. This seems reasonable for abundance measures such as percentage cover. For other abundance measures, such as stem counts, other error distributions may be more appropriate (cf. Austin and Cunningham 1981); such alternatives were not explored in the present study. When adding sampling errors, any data values made negative by the subtraction of a large random error are replaced by zero. Similarly, values greater than 100 are replaced by 100.

2.1.5.5 Cutoff for Small Values

The final adjustment applied to the data matrix is the replacement of all values less than some small cutoff value by zero. The normal value for the cutoff level is 0.001, although some other value may be specified. Very small values have little influence on the results of most ordination methods, although their inclusion may increase the cost of computation for some programs.

In the final data matrix it is possible for some species to be absent from all samples (due to competition adjustments or noise). Such species are deleted before the data matrix is filed.

2.1.6 Programs

The procedures outlined above have been embodied in two suites of computer programs, one for the simulation of coenoclines and the other for coenoplanes. Each suite consists of three programs. The first assigns parameters for physiological response profiles, the second allocates sample positions and the third uses output files from the first two programs and user-supplied options to create artificial data matrices. This modular design is similar to that adopted by Gauch and Whittaker (1976). It allows great flexibility in the separate development and combination of species sets and sampling schemes. The programs are written in portable FORTRAN and source listings will be made available on request.

2.2 Assessment of Fit

One of the major difficulties in synthesising the results of previous comparative ordination studies is the lack of uniformity in methods for assessing the fit of ordination configurations to the positions of samples in the models. Furthermore, some of the proposed measures of fit are extremely insensitive (see section 1.2).

The approach adopted in the present study is that suggested by Fasham (1977). This involves the use of Procrustean analysis (Schoneman and Carroll 1970), in order to bring the ordination configuration into optimal agreement with the arrangement of samples in the model. A graphical illustration of the procedure is given in Figure 2.3. The configuration at the upper left of the figure (open circles) represents a set of nine samples arranged in a regular grid on a model coenoplane.

The projections of the samples on the first two axes of an hypothetical ordination of the data are shown at the top right (closed circles). Although the relative positions of samples in the ordination reflect their locations in the model quite well, the ordination configuration is rotated somewhat with respect to the "true" configuration. Furthermore, the scaling of the ordination axes is such that the ordination configuration is "smaller" than the true configuration.

At the bottom of Figure 2.3, the result of Procrustean fitting of the ordination to the "true" configuration is shown. Corresponding points are joined by lines. The ordination has been transformed by a combination of origin translation, rotation of axes and uniform rescaling (in this case expansion), such that the sum of the squared distances between sample points in the ordination and their corresponding positions in the true configuration is minimised. The square root of the mean of these squared distances (i.e. the RMS average of the displacements) is used as a goodness-of-fit measure. This measure shall henceforth be referred to as the "RMS displacement error" and will be represented by the abbreviation Dn. The subscript n is an integer, specifying the dimensionality in which the fit was performed. Procrustean analyses were performed using the general statistical program GENSTAT (Nelder et al. 1977).

For ordinations of model coenoclines, RMS displacement errors were computed in both one and two dimensions. The D1 values express the accuracy with which the relative positions of samples are recovered on the first ordination axis. D2 reflects also the degree to which sample positions on the first two ordination axes depart from a linear

arrangement. In computing D2, the co-ordinates of all samples on the second axis of the "true" configuration were simply set to zero. A major limitation of D2 in this context is that it gives no indication of the extent to which displacement errors in two dimensions reflect systematic (e.g. curvilinear) departures from the expected linear arrangement, rather than random scatter into a second dimension.

For ordinations of data from simulated coenoplanes, RMS displacement errors were computed in both two and three dimensions. For coenoplanes in which the beta diversities of the axes were not equal, sample co-ordinates on each coenoplane axis were scaled in proportion to the beta diversity of that axis before Procrustean fitting of the ordination configurations.

In the special case of coenoclines, a measure was also required of the degree to which the first axis of an ordination preserves the rank order of samples along the coenocline. Preservation of rank order is a weaker requirement than the accurate representation of relative sample positions measured by D1. There are a number of non-parametric measures of the agreement between two orderings. The present study follows Fasham (1977) in using the Kendall rank correlation coefficient (Kendall 1938), which is often represented as τ (tau). Values of τ were computed using an original FORTRAN program incorporating the IMSL subroutine NMKEN (International Mathematical and Statistical Libraries, Inc. 1980).

The computation and comparison of performance statistics was supplemented by the inspection of plots of the ordination configurations. Plotting programs were written with the help of the FORTRAN subroutine library PLOT79 (Beebe 1979). Special FORTRAN

programs were written to convert the output of the various ordination programs employed in the study into a standard form for input to the plotting programs.

2.3 Ordination Techniques Evaluated

The ordination techniques compared in the present study were as follows :

(1) Detrended Correspondence Analysis (DCA), using the program DECORANA (Hill 1979a) with the default option settings.

(2) Principal Components Analysis (PCA), using an original FORTRAN program, incorporating the eigenanalysis subroutine EIGRS from the IMSL library (International Mathematical and Statistical Libraries, Inc. 1980). PCA was applied with each of three data adjustments. These were : (a) unstandardised, centred by species, (b) centred by species and standardised by species standard deviation and (c) Bray-Curtis double standardisation followed by centring by species. These ordinations will henceforth be represented by the abbreviations PCA-C, PCA-CS and PCA-BC respectively.

(3) Principal Co-ordinates Analysis (PCoA), using an original FORTRAN program incorporating the same eigenanalysis subroutine used for PCA. PCoA was applied to a matrix of percentage similarity coefficients (Appendix A, equation A1), computed between each pair of samples, using another original FORTRAN program.

(4) Non-Metric Multidimensional Scaling (NMDS), using the program KYST (Kruskal, Young and Seery 1973). The method was applied in its "local" form (Sibson 1972; Prentice 1977,1980), with primary

treatment of tied similarity values (see Appendix A, section A.6). "Local" scaling is selected in the program KYST using the option "SPLIT BYROWS". Euclidean distance was employed as the distance metric in the ordination. The input data was a matrix of percentage similarity coefficients between each pair of samples. Both self-comparisons and zero similarities between samples with no species in common were marked as "missing". Coenocline data were ordinated in both one and two dimensions and NMDS ordinations of coenoplane data were performed in both two and three dimensions. In all cases, DCA ordinations were used to supply starting configurations for NMDS. The abbreviation LNMDS will be used hereafter to refer to the "local" variant of NMDS, with the dimensionality of the ordination given in parentheses. For example, LNMDS(1D) represents a "local" NMDS in one dimension.

(5) Gaussian Ordination, using Cornell Ecology Program 8B (Gauch 1979). This technique was applied only to coenocline data, since it is not appropriate when there is more than one major underlying gradient. The program was redimensioned to allow analysis of up to 90 samples and 90 species. For data sets with more than 90 species, a modified version of Cornell Ecology Program 8A (Gauch 1979) was used to produce a reduced data matrix, comprising those 90 species with the highest variances. Scores on the first axis of the corresponding DCA ordination were used as the starting configuration for all Gaussian ordinations. The abbreviation GO is used hereafter for Gaussian Ordination.

Two other techniques were initially applied to a number of data sets. These were Parametric Mapping, using the program PARAMAP (Chang

1969), and Maximum Likelihood Non-linear Ordination (Goodall and Johnson 1982), using the program MAXMIN, kindly made available by the authors. Parametric Mapping performed badly in the initial trials. Problems were encountered with local minima and in many ordinations a few points were isolated from the remainder. Gauch, Whittaker and Singer (1981) reported a similar phenomenon, which they considered to be the result of points "lagging behind" in the iterative process. However, in the present study the method isolated points even when started with the "true" configuration. Computational problems were also encountered with some parameter settings, the program PARAMAP failing due to exponent overflow. In view of these problems and the considerable computational cost of PARAMAP, it was decided not to include Parametric Mapping in the main study.

Initial trials of Maximum Likelihood Non-linear Ordination revealed that the method used in the program MAXMIN to fit regressions for the transformed species abundance data (see Goodall and Johnson 1982) was extremely sensitive to small abundance values. The authors of the method were informed of the problem, and a weighted regression approach was incorporated into the program in an attempt to correct it (R.W. Johnson, personal communication 1983). Unfortunately, a workable version of the program was not available in time for the method to be included in the present study.

The ordination methods chosen for inclusion in this study represent a reasonable cross-section of the range of techniques currently used in plant ecology. Notable exclusions are Reciprocal Averaging (RA) and Wisconsin comparative or Polar Ordination (PO). RA was not considered here, since it appears to have been effectively

superseded by DCA, for the purpose of indirect gradient analysis (Hill and Gauch 1980; Gauch, Whittaker and Singer 1981). Polar Ordination was not included in the present study, since it was not regarded as a strictly indirect ordination technique (see section 1.6.1).

CHAPTER 3 : EXPERIMENTS WITH SIMULATED COENOCLINES

3.1 Introduction

The flexibility of the coenocline simulation programs designed for use in this study allows so many characteristics of coenoclines to be varied that it would be a practical impossibility to study the effects on ordinations of variation in all such characteristics in every possible combination. It has therefore been necessary to concentrate on a limited number of coenocline properties and their interactions.

The amount of variability between "replicate" coenoclines, generated with identical parameters but different random number seeds, makes replication highly desirable in studies of this type. Unfortunately, the practicalities of computing have necessitated a choice between an intensive, replicated study of the effects of variation in one or two coenocline properties and a more extensive study, involving a greater number of coenocline characteristics, but largely without replication. The latter course of action was adopted.

For the sake of brevity, ordination techniques will be referred to throughout chapters 3 and 4 by the abbreviations given in section 2.3.

3.2 Experiment 1 : The Effects of Beta Diversity, Quantitative Noise and Qualitative Noise with Symmetrical Response Curves

3.2.1 Introduction

This experiment examines the effects of beta diversity, quantitative noise and qualitative noise (using the probability of occurrence profiles), in all factorial combinations, on ordinations of data from simulated coenoclines with symmetrical, bell-shaped response curves for all species. The effects of variation in the first two of these properties, on the performance of some of the ordination techniques compared here, have been the subject of a number of earlier studies employing Gaussian coenoclines (Gauch and Whittaker 1972b; Kessell and Whittaker 1976; Gauch, Whittaker and Wentworth 1977). The results of these studies have been reviewed in Chapter 1. The present experiment is the first to compare such a wide range of ordination techniques simultaneously with uniform models and methods for assessing ordination success. The effect of qualitative noise does not appear to have been investigated previously.

Since the symmetrical beta functions used ($\alpha=4,\gamma=4$) are similar in shape to the Gaussian curve (Figure 3.1), this experiment may, in part, be expected to confirm the results of earlier studies using Gaussian models.

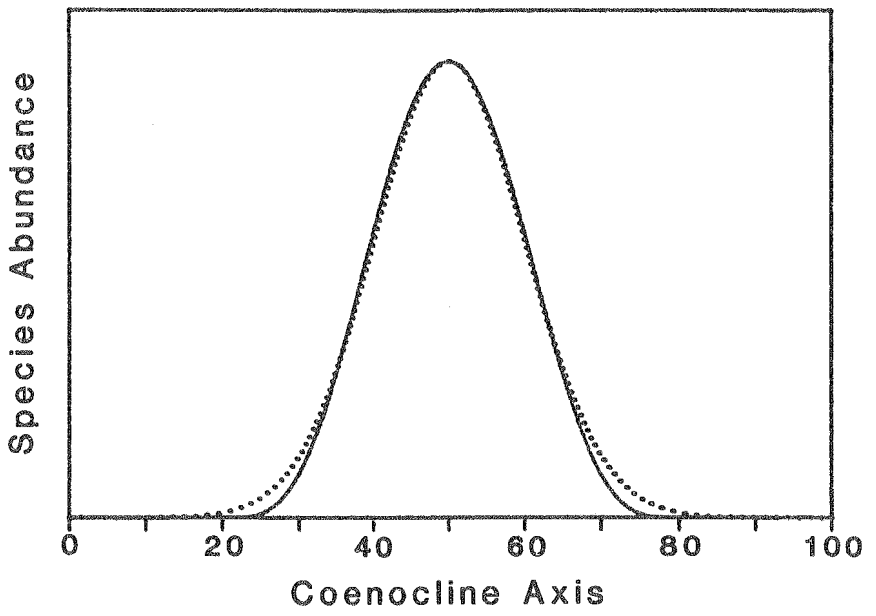


Figure 3.1 Graphical comparison of a symmetrical beta function ($\alpha=\gamma=4$) with a range of 60 units (solid line) and a Gaussian curve with a standard deviation of 10 units (dotted line), both curves having the same optimum position and height. Note that the curves are very similar in shape, the main discrepancy being that the Gaussian curve has more extended tails.

3.2.2 Methods

A series of five coenoclines were produced, with average abundance curve ranges of 400, 200, 100, 50 and 25 units, corresponding to beta diversities of 1.5, 3, 6, 12 and 24Z. The following coenocline characteristics were treated similarly in all five models :

(1) The standard deviation of the ranges of response curves was set at 0.3 times the average value.

(2) Modal abundances (AO) were assigned randomly from a lograndom distribution, on the range 1 to 100.

(3) Modal probabilities of occurrence (PO) were assigned using the default frequency distribution (Table 2.1).

(4) No segmentation of the gradient was performed for the purpose of allocating the positions of species modes, thus alpha diversity or species richness does not vary systematically along the gradient in these models.

(5) Those 15% of species whose abundance profiles had the largest integrals were designated as "major" and the modes of "major" species were readjusted to ensure more even spacing.

(6) Powers α and γ were set at 4.0 for all species.

The total number of species in each coenocline was chosen by trial and error, to ensure that the average number of species per sample (alpha diversity) was about 25 in the absence of noise. Previous studies have generally used the same total number of species in each of a series of models with increasing beta diversity. This approach confounds the effect of an increase in beta diversity with that of decreasing alpha diversity.

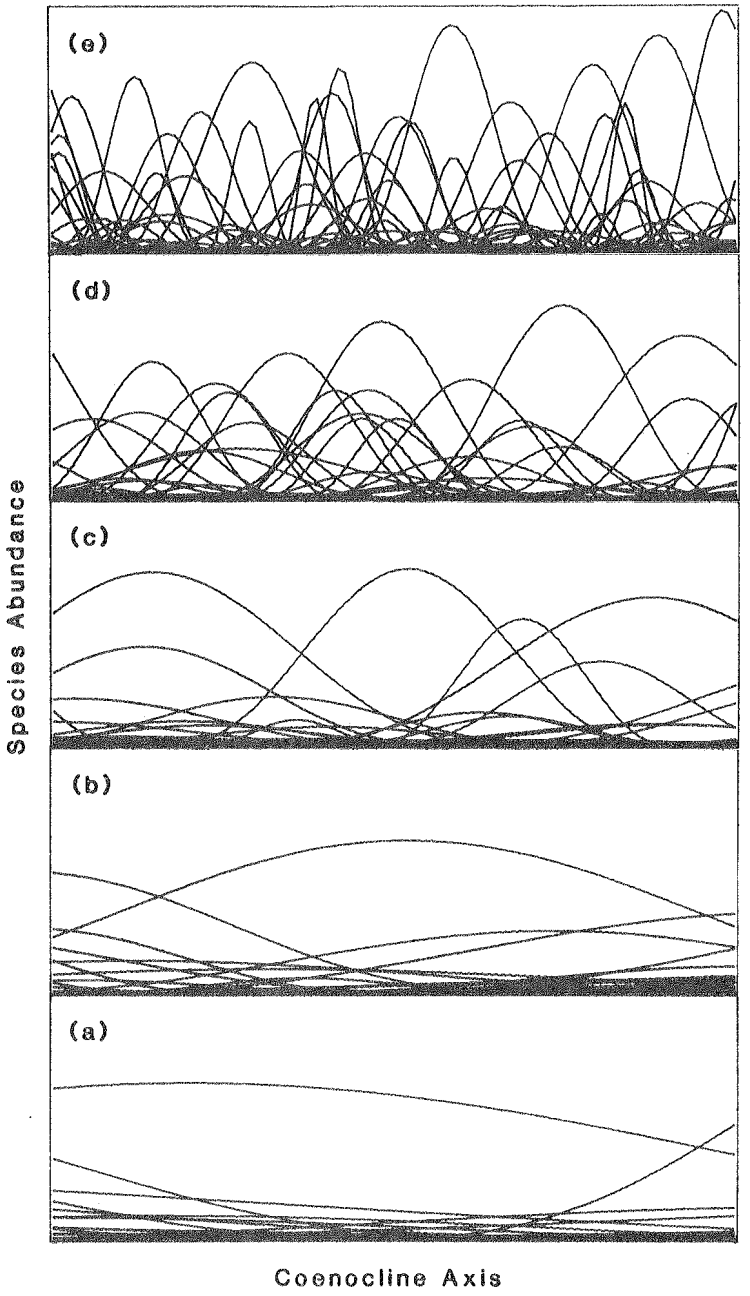


Figure 3.2 Species abundance profiles along the five noiseless coenoclines used in experiment 1. Beta diversities are as follows: (a) 1.5Z, (b) 3Z, (c) 6Z, (d) 12Z and (e) 24Z. The total number of species in each model was increased from (a) to (e), in order to maintain a constant alpha diversity of about 25 species per sample.

From each simulated coenocline, six data matrices were produced, representing all factorial combinations of three quantitative noise levels (0.0,0.1 and 0.2F) and the introduction or otherwise of qualitative noise. This gave a total of 30 data sets. Each model was sampled at 40 points, evenly spaced along the simulated coenocline. The abundance profiles of species in each of the five "noiseless" models are illustrated in Figure 3.2.

Each of the 30 data sets was ordinated by the range of techniques listed in section 2.3. Performance statistics D1, D2 and τ (section 2.2) were computed and plots of the ordination configurations were prepared.

3.2.3 Results

Performance statistics for the ordinations are given in Tables 3.1 and 3.2. When considering RMS displacement errors (D1 and D2), it should be borne in mind that the distance between adjacent samples in all coenoclines was 2.5 units. Ordination configurations for the noiseless data sets are shown in Figures 3.3 and 3.4.

In the absence of both qualitative and quantitative noise, all the ordination techniques studied performed reasonably well on the 1.5Z coenocline. Only PCoA failed to place all samples in the correct rank order along the first ordination axis (τ=0.98), due to slight involution of the extremes of the gradient (Figure 3.3). D1 values indicate that the accuracy of recovery of sample positions on the first ordination axis was worst for PCA-C and PCoA, with GO performing best of the remaining techniques. Two-dimensional ordinations by PCoA and the three

Ordination[1] Method	Performance[1] Statistic	Without Qualitative (Presence-Absence) Noise														
		Noise Level 0.0F					Noise Level 0.1F					Noise Level 0.2F				
		Beta Diversity (Z)					Beta Diversity (Z)					Beta Diversity (Z)				
		1.5	3.0	6.0	12.0	24.0	1.5	3.0	6.0	12.0	24.0	1.5	3.0	6.0	12.0	24.0
DCA	τ	1.00	1.00	1.00	1.00	1.00	0.95	0.98	0.99	1.00	1.00	0.91	0.93	0.98	1.00	1.00
	D_1	3.1	2.9	3.1	1.1	0.9	4.6	3.5	3.1	1.2	0.9	6.0	4.6	3.7	1.5	1.1
	D_2	2.4	11.0	7.6	6.0	4.0	7.7	6.2	5.9	4.3	4.1	10.6	8.0	6.1	5.4	4.3
PCA-C	τ	1.00	0.91	0.69	0.25	0.26	0.90	0.89	0.70	0.28	0.28	0.86	0.72	0.72	0.24	0.45
	D_1	5.9	10.0	10.7	22.8	20.3	8.5	10.2	10.7	21.3	20.3	10.3	12.7	10.6	24.0	20.4
	D_2	13.2	15.5	18.3	23.1	23.6	14.5	16.1	18.6	22.8	23.4	15.8	18.1	18.4	23.4	24.5
PCA-CS	τ	1.00	1.00	0.97	0.75	0.74	0.92	0.93	0.90	0.65	0.82	0.88	0.90	0.89	0.71	0.74
	D_1	2.8	3.8	5.6	10.8	13.5	5.0	5.6	5.9	12.5	11.2	9.7	5.7	6.4	11.8	16.3
	D_2	11.3	14.3	17.7	20.4	21.3	13.5	15.8	17.6	20.4	20.9	15.4	16.2	17.3	20.3	22.0
PCA-BC	τ	1.00	0.90	0.85	0.59	0.59	0.85	0.87	0.80	0.59	0.60	0.84	0.79	0.78	0.59	0.52
	D_1	3.4	7.9	8.1	14.6	15.7	7.7	8.1	9.0	15.0	15.8	7.8	10.0	9.2	15.1	16.7
	D_2	12.4	16.3	17.7	21.5	22.8	14.9	17.5	18.4	21.6	22.8	16.8	18.4	17.7	21.7	22.8
PCoA	τ	0.98	0.96	0.79	0.67	0.52	0.91	0.93	0.81	0.66	0.56	0.89	0.85	0.85	0.66	0.52
	D_1	5.1	6.6	8.5	12.1	16.4	6.9	7.8	8.7	12.5	15.8	6.1	9.1	8.3	12.4	16.7
	D_2	15.2	16.7	17.9	21.0	22.6	15.0	16.9	18.0	21.0	22.5	16.2	17.1	17.7	21.0	23.0
LNMDS (1D)	τ	1.00	1.00	1.00	1.00	1.00	0.94	0.98	0.99	0.99	1.00	0.91	0.89	0.97	0.99	1.00
	D_1	3.5	3.4	3.3	2.2	1.9	6.1	4.3	4.0	2.0	1.4	8.6	6.2	4.7	2.6	1.2
LNMDS (2D)	τ	1.00	1.00	0.99	1.00	1.00	0.93	0.97	0.97	0.99	1.00	0.91	0.88	0.94	0.98	1.00
	D_1	3.5	4.1	4.3	2.8	1.2	5.9	4.6	4.8	2.6	1.6	7.9	6.5	5.5	2.8	1.8
	D_2	3.7	11.1	7.5	9.1	3.5	8.2	7.9	8.2	8.7	3.6	11.4	10.2	9.2	8.5	4.7
GO	τ	1.00	1.00	1.00	1.00	1.00	0.87	0.94	0.98	1.00	1.00	0.60	0.85	0.93	1.00	0.99
	D_1	2.2	0.9	2.4	1.0	0.8	8.7	4.2	3.0	1.1	1.0	18.6	7.3	4.4	1.5	1.1

[1] For the meanings of the abbreviations used for ordination techniques and details concerning the performance statistics used, see Chapter 2.

Table 3.1 Ordination performance statistics for experiment 1, in which simulated coenoclines were used to investigate the joint effects of beta diversity, quantitative noise and qualitative noise on ordination. The results presented are for those models with no qualitative noise introduced. Species in all models had symmetrical, bell-shaped response curves.

Ordination Method	Performance Statistic	With Qualitative (Presence-Absence) Noise														
		Noise Level 0.0F					Noise Level 0.1F					Noise Level 0.2F				
		Beta Diversity (Z)					Beta Diversity (Z)					Beta Diversity (Z)				
		1.5	3.0	6.0	12.0	24.0	1.5	3.0	6.0	12.0	24.0	1.5	3.0	6.0	12.0	24.0
DCA	τ	0.70	0.85	0.93	0.97	0.99	0.64	0.84	0.88	0.98	0.99	0.66	0.84	0.87	0.97	0.98
	D_1	18.0	9.5	5.8	3.7	1.6	19.0	9.2	6.3	2.0	1.8	18.5	11.8	6.9	3.3	2.6
	D_2	23.5	14.5	8.4	5.0	4.6	22.7	13.5	8.6	4.1	2.9	22.8	15.5	10.2	5.5	4.2
PCA-C	τ	0.64	0.04	0.66	0.19	0.42	0.45	0.37	0.66	0.26	0.07	0.30	0.25	0.72	0.25	0.25
	D_1	25.2	28.5	14.9	24.4	22.9	25.6	22.2	14.4	23.9	26.2	26.7	25.3	13.6	24.2	24.8
	D_2	25.3	24.1	20.9	26.4	25.0	25.9	21.9	20.4	24.3	24.8	26.0	23.7	21.0	23.6	24.3
PCA-CS	τ	0.77	0.90	0.79	0.55	0.24	0.69	0.81	0.82	0.46	0.73	0.69	0.82	0.79	0.34	0.52
	D_1	13.2	8.9	9.8	16.2	25.9	15.6	10.5	8.7	18.1	18.1	18.9	12.1	11.6	20.3	23.8
	D_2	19.6	17.5	18.8	21.8	26.2	22.3	17.6	19.2	22.0	21.9	22.9	20.7	19.7	22.3	26.2
PCA-BC	τ	0.68	0.67	0.70	0.62	0.49	0.25	0.54	0.69	0.65	0.45	0.20	0.05	0.64	0.49	0.43
	D_1	16.8	11.7	12.1	14.7	19.9	25.1	16.1	13.4	14.5	24.9	27.5	26.8	14.3	17.6	21.3
	D_2	22.6	20.1	20.1	22.1	23.8	24.0	21.0	20.6	21.6	26.0	25.6	22.8	20.4	22.2	24.8
PCoA	τ	0.37	0.66	0.74	0.52	0.53	0.29	0.64	0.75	0.67	0.42	0.21	0.37	0.75	0.47	0.75
	D_1	26.3	15.2	11.0	16.3	19.9	25.6	15.1	11.1	13.2	20.3	27.7	21.7	10.3	16.6	14.8
	D_2	23.7	21.2	20.3	21.9	24.2	25.0	20.1	19.9	21.3	22.7	25.5	22.2	19.8	21.8	22.4
LNMDS (1D)	τ	0.66	0.79	0.92	0.97	0.98	0.58	0.76	0.84	0.98	0.98	0.22	0.75	0.82	0.97	0.97
	D_1	26.2	14.0	6.2	3.4	2.5	26.7	18.7	8.1	2.8	1.9	28.2	16.2	8.1	3.3	2.9
LNMDS (2D)	τ	0.37	0.82	0.89	0.96	0.98	0.49	0.79	0.86	0.97	0.98	0.23	0.82	0.86	0.96	0.97
	D_1	27.3	10.9	7.5	3.4	2.6	25.2	13.6	7.8	3.1	2.0	28.2	13.8	6.3	3.3	2.5
	D_2	24.9	17.2	15.7	7.2	5.4	25.1	18.0	13.7	8.0	4.5	25.5	18.6	12.8	6.4	5.4
GO	τ	0.82	0.95	0.96	0.99	0.99	0.66	0.92	0.94	0.99	0.99	0.58	0.84	0.91	0.96	0.97
	D_1	13.2	6.3	4.6	3.3	1.4	17.0	4.7	4.0	1.8	1.9	22.4	10.2	4.9	3.5	3.4

Table 3.2 Ordination performance statistics for experiment 1, in which simulated coenoclines were used to investigate the joint effects of beta diversity, quantitative noise and qualitative noise on ordination. The results presented are for those models with qualitative noise introduced. Species in all models had symmetrical, bell-shaped response curves.

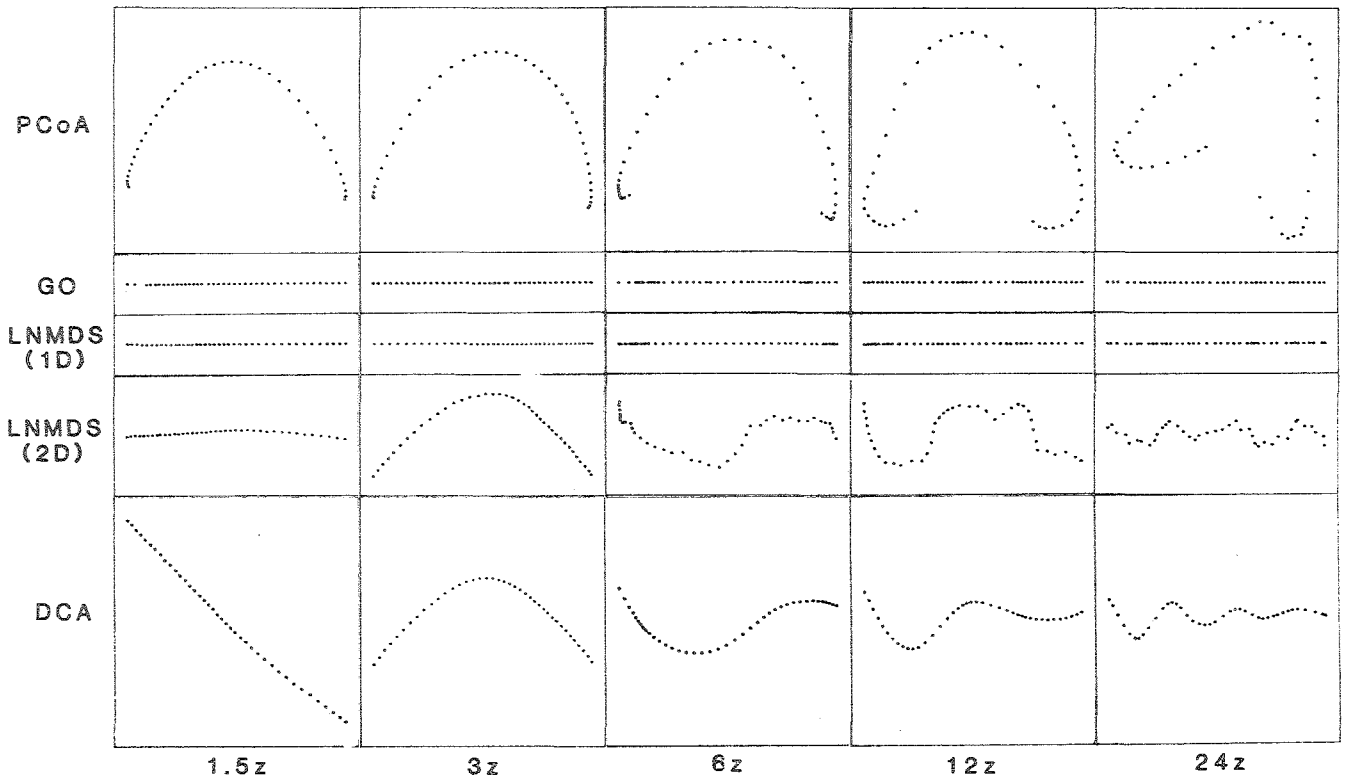


Figure 3.3 Ordinations of the noiseless data sets from the five model coenoclines of increasing beta diversity in experiment 1. The results shown are for the ordination techniques PCoA, GO, LNMDS(1D and 2D) and DCA. The plots for GO and LNMDS(1D) are unidimensional, since each of these methods produces only a single ordination axis. For the other methods, sample locations on the first two ordination axes are illustrated. Results for the three PCA variants are given in Figure 3.4.

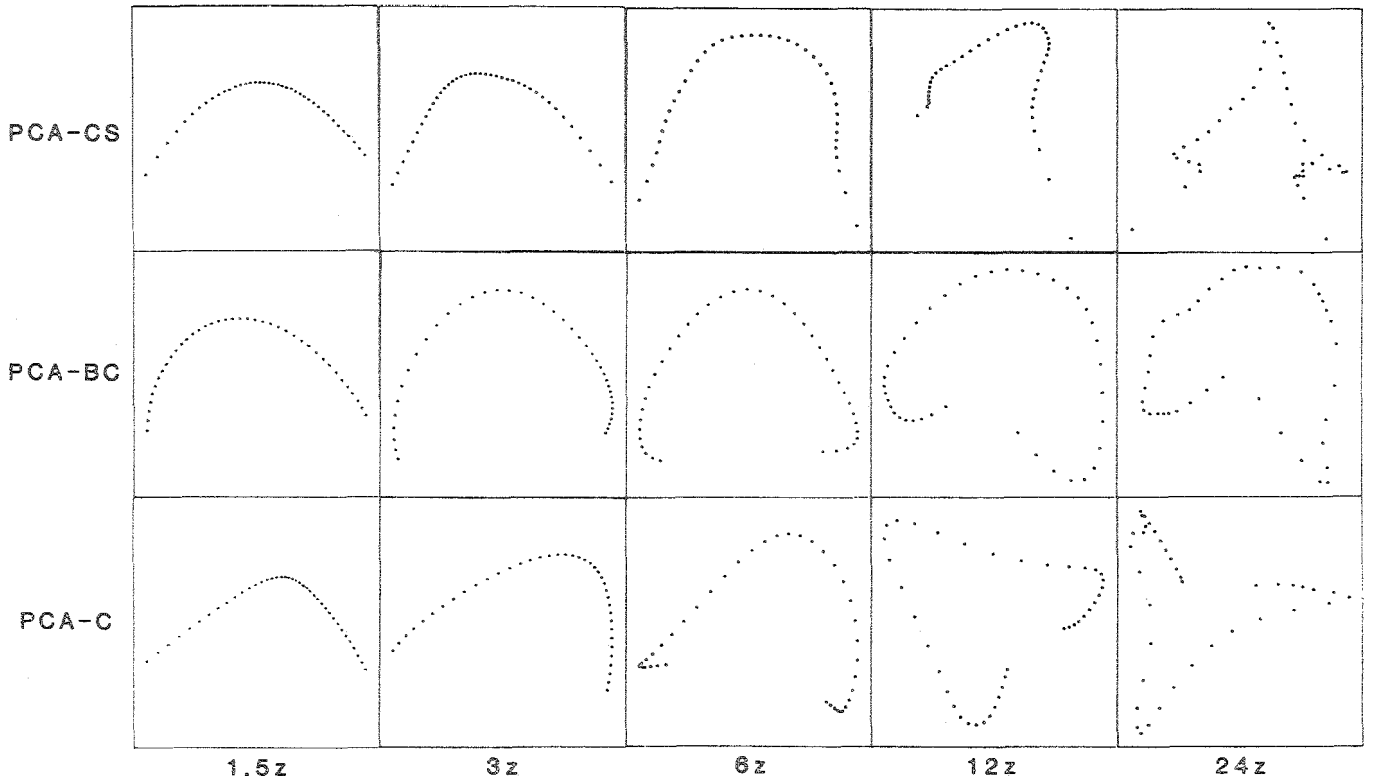


Figure 3.4 Ordinations of the noiseless data sets from the five model coenoclines of increasing beta diversity in experiment 1. The plots show sample positions on the first two ordination axes for the three variants of PCA examined. Results for the other methods compared are given in Figure 3.3.

PCA variants showed moderate curvature of the coenocline into an approximately parabolic arch. D2 values for these methods partly reflect the degree of curvature. The two-dimensional ordinations by both DCA and LNMDS(2D) were remarkably linear, however sample scores on the second axis of the DCA ordination bore a strong, approximately linear relationship to those on the first (Figure 3.3). This suggests a failure of the detrending procedure at low beta diversities. Nevertheless, the ratio of the eigenvalue on the first DCA axis to that on the second was 50.6, clearly indicating a unidimensional solution. Re-running of the DCA ordination with the number of segments for detrending set at 50 (the maximum allowable in the program DECORANA), as suggested by Hill (1979a), reduced but did not eliminate the monotonic relationship between the second and first axes.

The techniques studied fall into two groups with regard to their response to increasing beta diversity. Those in the first group, which comprises PCoA and the three PCA variants, displayed increasing curvature of the coenocline as the beta diversity increased, with consequent involution of the extremes of the gradients and failure to recover the correct rank order of samples on the first axis. PCA-C was worst affected in this respect. Two-dimensional ordinations of the 12 and 24Z coenoclines by PCA-C showed a complex arrangement of spikes and folds (Figure 3.4). PCA-BC and PCoA appeared to be about equally affected by increasing beta diversity, while PCA-CS performed best of the techniques in this group. The latter method was resistant to involution at 3Z and the rate of increase in curvature with increasing beta diversity was less than that observed for the other three techniques.

Ordination methods in the second group, comprising DCA, LNMDS(1D and 2D) and GO, behaved quite differently. Rank order recovery by DCA was perfect over the entire range of beta diversity studied, and D1 values decreased with increasing beta diversity. DCA ordinations were used as starting configurations for both LNMDS and GO. When allowed one dimension, LNMDS preserved the correct rank order of samples, but RMS displacement error (D1) increased slightly (Table 3.1). In two dimensions, the accuracy of recovery of sample positions on the first axis deteriorated somewhat further. In the case of the 6Z coenocline, one extreme sample was placed out of order on the first axis. In contrast, GO not only preserved the correct rank order of samples, but also reduced D1 values somewhat, in comparison to DCA.

The introduction of quantitative sampling errors or noise resulted in the random displacement of samples from their positions in the corresponding ordinations of the "noiseless" models. For all methods, the effects of this noise-induced scatter were most apparent at low beta diversities (Table 3.1). Under such conditions, increasing levels of quantitative noise were associated with relatively large increases in D1 values and the failure of rank order recovery on the first axis. DCA and LNMDS were the least affected in this respect. GO was extremely sensitive to quantitative noise at low beta diversities. For the 1.5Z coenoclines with noise levels of 0.1 and 0.2F, GO ordinations had the highest D1 values of all methods tested. This contrasts sharply with the performance of GO on the noiseless coenoclines, where it was the most successful technique.

In models with beta diversities of 6Z or more, the effect of

quantitative noise was less marked. The greater degree of compositional variation between samples along coenoclines with higher beta diversity tends to outweigh the random variation due to noise (cf. Gauch, Whittaker and Wentworth 1977). DCA was the most resistant of all the techniques studied to the effects of quantitative noise at high beta diversities. For coenoclines of 12 and 24Z, DCA achieved perfect rank order recovery, even with noise levels of 0.2F, and RMS displacement errors (D1) approached those obtained in the absence of noise as beta diversity increased.

The impact of qualitative or presence-absence noise on ordinations was considerable, especially at the lowest beta diversities (Table 3.2). When qualitative noise was introduced without quantitative noise, the most successful of the techniques studied was GO. For beta diversities up to 6Z, GO was able to improve significantly upon the DCA solution, both in terms of rank order recovery and RMS displacement error. However, the advantage was trivial at beta diversities of 12 and 24Z. For the PCA and PCoA, the scatter introduced by qualitative errors was occasionally great enough to result in a totally spurious first axis, reflecting both random variation and curvilinear distortion of the underlying gradient. In such cases, the true gradient was (crudely) represented by the second ordination axis. A prime example of this phenomenon is the PCA-C ordination of the 3Z coenocline with qualitative noise but no quantitative noise (Table 3.2).

The simultaneous introduction of both qualitative and quantitative noise generally resulted in even greater scatter of points from their "noiseless" positions and consequently a further reduction in the performance of all techniques. For the series of models with

qualitative noise and a quantitative noise level of 0.1F, GO solutions had rank correlations higher and D1 values lower than the corresponding DCA ordinations when beta diversity was 6Z or less. Thus at this level of quantitative noise, the robustness of GO with respect to qualitative noise appears to outweigh its greater sensitivity to quantitative noise. For models of up to 6Z with the same level of quantitative noise, but without qualitative noise, GO was unable to improve on the DCA solutions (Table 3.1). When a quantitative noise level of 0.2F was applied simultaneously with qualitative error, the advantage of GO over DCA disappeared.

At beta diversities of 12Z or greater, and in the presence of qualitative noise, DCA was generally the most successful technique. DCA ordinations of such data sets had the lowest D1 values and the highest rank correlations. The addition of quantitative noise did not seriously reduce the performance of DCA under these conditions. Neither GO nor LNMDS was able to improve significantly on the DCA results for these noisy, high beta diversity models.

The combined effects of beta diversity, quantitative and qualitative noise on D1 values for DCA and PCA-CS ordinations are illustrated graphically in Figure 3.5. The general tendency for DCA ordinations to represent sample positions more accurately as beta diversity increases is readily apparent, as is the decreasing effect of both quantitative and qualitative noise towards higher beta diversities, and the drastic effect of qualitative noise at lower beta diversities. The results for PCA-CS are indicative of those for the other two PCA variants and PCoA. PCA-CS was chosen for illustration since it was the

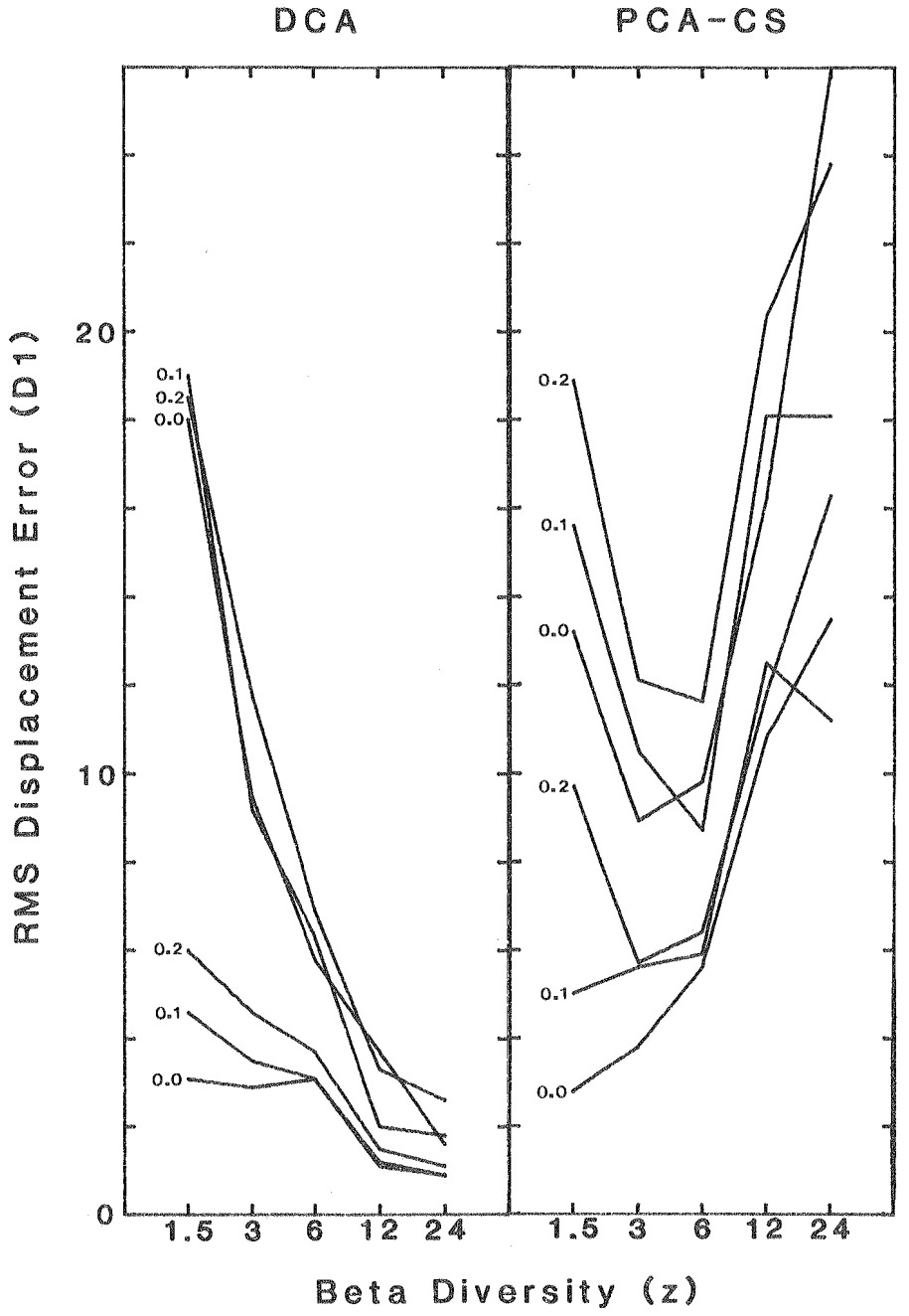


Figure 3.5 The joint effects of beta diversity, quantitative noise and qualitative noise on the accuracy of sample position recovery by DCA and PCA-CS in experiment 1. Each model had symmetrical, bell-shaped response curves for all species. Accuracy of sample position recovery is measured by the RMS displacement error, D_1, low values indicating greater accuracy. Quantitative noise levels in F units are indicated by the small numbers near the start of each curve. In both graphs, the upper set of three curves illustrates results for the data sets with qualitative noise added, while the lower three curves refer to data sets without qualitative noise.

most successful of the techniques in this group. RMS displacement errors for PCA-CS increase with beta diversity, primarily because of the increasing curvature and involution of the coenocline (Figure 3.4). In the presence of noise, D1 values for PCA-CS decrease initially up to a beta diversity of 3-6Z, then rise with a further increase in beta diversity. The initial improvement is due to a tendency for the greater compositional variation associated with gradients of moderate beta diversity to compensate to some extent for the random variation due to noise. However, this advantage is eventually outweighed by the curvilinear distortion of the gradient.

3.2.4 Discussion and Conclusions

Of the techniques compared, DCA was the most consistently successful with these symmetrical, unimodal models. DCA ordinations were not subject to severe curvilinear distortion of the underlying gradient and the consequent involution of extreme samples as beta diversity increases. In contrast, all three PCA variants and PCoA were affected by such involution. In the absence of noise, DCA always recovered the correct rank order of samples along the gradient on its first axis. DCA appeared fairly robust to the effects of quantitative noise at a beta diversity of 1.5Z and became increasingly so with increasing beta diversity (Figure 3.5). DCA also produced reasonable ordinations of coenoclines with a beta diversity of 6Z or more in the presence of qualitative error.

Both LNMDS and GO were provided with DCA solutions as starting configurations. Unidimensional ordinations by LNMDS generally failed to improve upon the DCA solution. LNMDS generally preserved a similar rank

order of samples, but produced higher values of D1. At beta diversities of 6Z or less and in the presence of qualitative noise, rank order recovery actually deteriorated in the LNMDS(1D) ordinations compared with the corresponding DCA solutions (Table 3.2). This suggests a greater sensitivity of LNMDS(1D) to qualitative noise at low beta diversities. Gauch, Whittaker and Singer (1981), working with Gaussian coenoclines, have also reported that ordinations by various types of Non-metric Multidimensional Scaling were generally inferior to those produced by DCA, although the results of Fasham (1977) show that global NMDS, using the cos-theta similarity coefficient, can produce more accurate ordinations of Gaussian coenoclines than Reciprocal Averaging.

When allowed two dimensions, LNMDS ordinations represented the coenoclines as curves (Figure 3.3), though not of the simple "arch" type typical of PCA and PCoA (Figures 3.3 and 3.4). Even in the absence of noise, a certain degree of irregularity in the relative placement of samples along the curve is apparent. In some cases, the LNMDS(2D) solutions appeared very similar to the original DCA solutions, suggesting the possibility of entrappment in a local minimum. Involution of the gradient extremes may occur, resulting in a reduction of the degree of rank order preservation as compared with the LNMDS(1D) ordinations. This highlights the fact, previously noted by other authors (e.g. Fasham 1977; Prentice 1980; Gauch, Whittaker and Singer 1981), that best results are attained with NMDS when the correct underlying dimensionality is specified.

In conrast to LNMDS(1D), GO was able to improve on the DCA solutions, but only in the absence of quantitative noise. The improvement in D1 values was most marked at the lower beta diversities

(Tables 3.1 and 3.2). Unfortunately, GO appeared very sensitive to quantitative noise at beta diversities less than 6Z. Thus the present results do not support the claim of Gauch, Chase and Whittaker (1974), that GO is robust to quantitative sampling errors. For a noise level of 0.2F, the GO ordination of the 1.5Z coenocline had by far the highest D1 value of all methods tested. On the other hand, GO proved less vulnerable to the effects of qualitative noise than DCA, presumably because zero values are ignored in the fitting of Gaussian regressions.

The present experiment confirms the results of several previous studies (section 1.5.1.1) in showing that PCA ordinations are increasingly afflicted by the curvilinear distortion of coenoclines as beta diversity increases. As discussed in section 1.5.1.1, the curvature is a consequence of the non-linearity of the response curves of species, which leads to a non-linear relationship between compositional dissimilarity (Euclidean distance) and ecological distance (coenocline separation). In the present study, PCoA (using the percentage similarity coefficient) was also shown to be affected by curvilinear distortion, with results generally intermediate between those of PCA-C and PCA-CS (Tables 3.1 and 3.2; Figure 3.3). It has been shown that the relationship between percentage similarity and the separation of samples along Gaussian coenoclines is curvilinear, the rate of decline in computed similarity increasing as sample separation increases (Gauch 1973a). PCoA attempts to position the samples such that their distances apart in the ordination are linearly related to their computed similarities. This can only be achieved by bending the coenocline into a curve.

The order of performance, from best to worst (in terms of τ and D1) of PCoA and the PCA variants in the present experiment was PCA-CS > PCA-BC = PCoA > PCA-C. Gauch, Whittaker and Wentworth (1977) also considered PCA-CS superior to PCA-C. One undesirable feature of PCA-CS, noted in the present study, is a tendency for samples located at or near the extremes of gradients to appear somewhat isolated from the remaining samples in the ordination. This "outlier" effect is clearly visible in the ordinations of the noiseless 6,12 and 24Z coenoclines by PCA-CS (Figure 3.4). The phenomenon is due to the occurrence in extreme samples of species whose frequency of occurrence in the sample set is low. These are species with modes located well beyond the ends of the gradient, with the tails of their response curves just entering the sampled region. The equalisation of species variances, implicit in PCA-CS, weights samples possessing several such "rare" species highly, (Noy-Meir, Walker and Williams 1975) and this makes such samples appear as relative outliers in the ordination. Despite the "outlier" effect, PCA-CS usually recovers the relative positions of samples more accurately at a given level of beta diversity than PCoA, PCA-CS or PCA-C, since it is more resistant to involution of the extremes of the coenocline. Standardisation by species standard deviation improves the performance of PCA by reducing the degree of curvature of the relationship between Euclidean distance and coenocline separation (cf. Gauch, Whittaker and Wentworth 1977). The present experiment therefore suggests that, if PCA is to be used for ecological ordination, the PCA-CS variant should give best results.

It has been suggested by some authors (Greig-Smith 1980; Feoli and Feoli Chiapella 1980) that the curvilinear distortion of underlying

compositional gradients in linear ordinations (e.g. PCA,PCoA) does not matter, provided that the interpretation of such ordinations takes full account of the likelihood of curvilinear distortion. They would presumably argue that the unidimensionality of the data could still be inferred, even though samples are arranged along a complex curve, and that the plotting of environmental variables on the ordination would reveal that the variation along the curve was related to a single underlying gradient. However, the present results indicate that the effects of noise can make the recognition of a single curved gradient difficult, especially at moderate to high beta diversities, when samples from different sections of the involuted gradient may be intermingled. When there is more than one underlying gradient, further difficulties arise; these will be discussed in the next chapter. There can be no doubt that the recovery of sample positions along a single underlying gradient on the first axis of an ordination, without systematic involution of gradient extremes (as is generally achieved by DCA) greatly simplifies the task of interpreting ordination results. It also reduces the likelihood of attempts to interpret totally spurious dimensions of variation.

This experiment has revealed one combination of circumstances in which none of the methods compared was particularly effective, namely at low beta diversities and in the presence of qualitative noise, with or without additional quantitative noise. Nevertheless, the results produced by DCA were generally superior to and in no case worse than those of PCoA, LNMDS and the three PCA variants under these circumstances.

In summary, the results of this experiment suggest that, when

species response curves are unimodal and symmetrical and there is a single underlying gradient, DCA is generally the most successful method of those tested. The symmetrical, unimodal species response models used in this experiment are highly compatible with the Gaussian model assumed by GO. Nevertheless, GO was able to improve significantly on DCA solutions only at moderate to low beta diversities, and then only in the absence of noise, or with qualitative noise only. LNMDS performed best when one dimension was specified, but it consistently failed to improve upon the DCA solutions. PCoA and PCA are only useful for ecological ordination at low beta diversities.

3.3 Experiment 2 : The Effect of Response Curve Shape

3.3.1 Introduction

This experiment examines the effects of variation in the shape of species response curves on the performance of ordination methods. Examination of the published results of direct gradient analyses reveals that curve shapes other than the unimodal, bell-shaped type are common (see also Chapter 8 of this thesis), and the preliminary experiments of Austin (1976b) suggest that a number of ordination methods may be undesirably sensitive to departures from the Gaussian form.

3.3.2 Methods

Since the previous experiment demonstrates that variation in beta diversity has drastic effects on the performance of some ordination methods, it may be thought desirable that the joint effects of beta diversity and curve shape be investigated. However, practical considerations have limited the examination of the effects of curve shape to a single level of beta diversity. The level chosen was 6Z. At this level of beta diversity, the average response curve range is equal to the total length of the coenocline. Hence the floristic gradient is just long enough for samples from opposite ends to have few, if any, species in common. It is likely that compositional gradients in many sets of field data (e.g. regional vegetation surveys) would be at least this length. Theoretical considerations suggest that the effects of variation in curve shape would become less pronounced at higher beta diversities, since most of the "information" would then be contained in the restriction of species to certain regions of the gradient. The shape of the abundance profiles may be relatively unimportant under these conditions. At low beta diversities, variation in curve shape may also be less important, since most species would be represented on the gradient by only one tail of their curve.

Six types of models were generated, with three replicates of each type being prepared using different sequences of random numbers. Details were as follows :

(1) Symmetrical - all species had symmetrical, unimodal response curves with powers α and γ equal to 4.0. Modal abundances were assigned from a lograndom distribution, on the range 1 to 100.

The standard deviation of abundance curve ranges was 0.3 times the average value. No segmentation of the coenocline was performed when allocating the positions of species modes. Those 15% of species with the largest abundance curve integrals were designated "major" and their modes were readjusted to ensure equitable spacing. These models were of the same type as the noiseless 6Z coenocline in experiment 1, and the model used in that experiment is designated as replicate number one here.

(2) Slightly Skewed - all species had response curves slightly skewed to the right, with powers α=4.0 and γ=2.0. Other details were the same as for the symmetrical models.

(3) Highly Skewed - all species had response curves highly skewed to the right, with powers α=4.0 and γ=1.0, other details being the same as for the symmetrical models

(4) Mixed Skewness - response curves for each species had both powers α and γ randomly selected on the range 1.0 to 4.0. This resulted in a range of curve shapes, varying from symmetrical to highly skewed in either direction. Once again, the other details were the same as in the symmetrical models.

(5) Competition Models with Symmetrical Physiological Response Curves- "physiological" response curves for each species were symmetrical, with powers γ and α of 4.0. The standard deviation of species ranges was set at 0.5 times the average value and modal abundances were assigned from a lograndom distribution on the range 5 to 100. The modes of "major" species were not readjusted. Competition was introduced in the form of randomly assigned linear interaction coefficients (as described in Section 2.1.5.1). The upper limit for the coefficients, Cmax, was set at 0.4, and the "protection

factor" for minor species, Clim, was given a value of 0.4. Parameter distributions for the "physiological" response curves and the values of the competition parameters (Cmax, Clim) were chosen by trial and error, in order to produce final "ecological response curves" approaching the types often observed in direct gradient analyses. Although the "physiological" curves were symmetrical and unimodal, the resulting ecological response curves were often skewed or shouldered and sometimes bimodal or multimodal.

(6) Competition Model with Skewed Physiological Response Curves - these models were similar to those just described, but with skewed "physiological" abundance profiles, obtained by setting powers α=2.0 and γ=1.0, for all species. All other parameter settings were identical to those used in the competition models with symmetrical physiological response curves.

Figure 3.6 illustrates the form of species response curves in one of the three replicates for each of the six types of models.

Beta diversities were set at 6Z in all models, giving an average abundance curve range of 100 units. In the competition models (types (5) and (6)), interaction between species generally truncated the ranges of all species to some degree, hence the beta diversities of these models were effectively somewhat higher. The total number of species in each model was selected by trial and error, in order to produce an average number of species per sample (alpha diversity) of about 25. In all models, 40 samples were evenly spaced along the simulated gradient. Each of the 18 data sets was ordinated using the set of methods listed in section 2.3, and performance statistics were computed. Plots of the

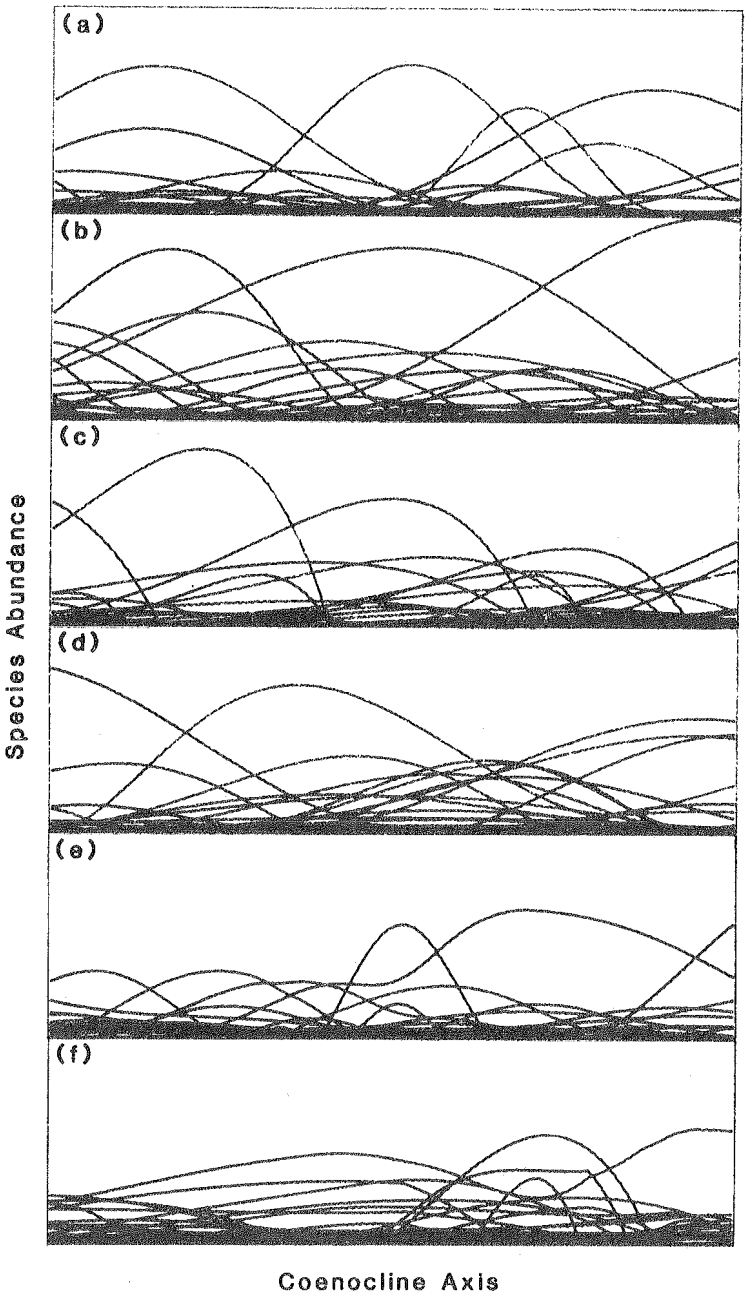


Figure 3.6 Species abundance profiles along some of the model coenoclines used in experiment 2 to assess the effects of variation in response curve shape on the performance of ordination methods. The coenoclines illustrated represent one replicate from each of the response curve shape categories examined. These are: (a) symmetrical, (b) slightly skewed, (c) highly skewed, (d) mixed skewness, (e) competition models derived from symmetrical physiological response curves and (f) competition models derived from skewed physiological response curves. Further details of model construction are given in the text.

ordination configurations were prepared and inspected.

3.3.3 Results

Performance statistics are presented in Table 3.3. As in experiment 1, the interpretation of D1 and D2 values should take into account the fact that the separation of adjacent samples was 2.5 units in each model. PCA-C, PCA-BC and PCoA ordinations were consistently afflicted by involution at this level of beta diversity, and their performance, as expressed by τ and D1, did not improve significantly with variation in curve shape. Hence the results for these methods will not be described further. Similarly, the two-dimensional ordinations by LNMDS will not be considered in detail. They were generally inferior to the unidimensional solutions, with rank order recovery deteriorating because of slight involution of the extreme samples.

With symmetrical response curves, DCA always achieved perfect rank order recovery on its first axis and this order was maintained by both LNMDS(1D) and GO. LNMDS(1D) failed to improve the accuracy of the recovery of sample positions (as expressed by D1), although GO succeeded in improving the fit for all three replicates. PCA-CS achieved perfect rank order recovery and a reasonable fit for replicate 3.

With slightly skewed curves, DCA, LNMDS(1D) and GO achieved perfect rank order recovery in all cases. LNMDS(1D) reduced the value of D1 for replicate 3 and GO managed to improve the fit for replicate 2. The consistent advantage of GO over DCA thus disappeared when curves were not symmetrical, as assumed in the fitting of regressions in GO.

For the models with highly skewed curves, DCA and LNMDS(1D) again

Ordination Method	Performance Statistic	Symmetrical ($\alpha=\gamma=4$)			Slightly Skewed ($\alpha=4,\gamma=2$)			Highly Skewed ($\alpha=4,\gamma=1$)			Mixed Skewness ($\alpha=1\text{-}4,\gamma=1\text{-}4$)			Competition Model with Symmetrical Physiological Curves			Competition Model with Skewed Physiological Curves		
		Replicates			Replicates			Replicates			Replicates			Replicates			Replicates		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
DCA	τ	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00	0.98	1.00	0.99
	D_1	3.1	1.5	1.7	1.7	3.6	1.4	3.1	1.8	2.1	1.2	1.4	2.8	3.0	4.0	3.4	5.2	3.6	4.3
	D_2	7.6	6.2	7.5	9.0	9.3	10.7	9.3	7.1	7.8	12.8	9.7	10.4	7.9	11.4	6.2	13.3	7.9	6.6
PCA-C	τ	0.69	0.89	0.98	0.89	0.74	0.60	0.65	0.65	0.86	0.85	0.67	0.82	0.62	0.87	0.67	0.69	0.90	0.37
	D_1	10.7	7.4	5.0	6.8	9.8	12.5	12.7	13.4	7.5	8.3	11.6	10.8	12.7	8.3	12.9	21.4	10.6	21.4
	D_2	18.3	19.9	19.6	16.8	15.0	18.5	19.8	19.4	17.1	18.5	15.5	14.2	18.8	16.8	19.0	21.8	17.4	22.9
PCA-CS	τ	0.97	0.79	1.00	0.98	1.00	1.00	1.00	0.98	1.00	0.64	1.00	1.00	0.88	1.00	0.95	1.00	1.00	1.00
	D_1	5.6	15.0	3.1	9.1	4.4	7.2	6.0	11.5	9.3	15.0	3.6	3.0	8.4	5.0	6.9	3.6	5.4	2.7
	D_2	17.7	18.8	17.3	19.7	17.4	18.5	17.1	17.4	17.4	19.6	16.3	16.3	16.7	19.4	18.1	17.3	17.8	17.3
PCA-BC	τ	0.85	0.74	0.73	0.85	0.63	0.76	0.75	0.69	0.71	0.94	0.75	0.78	0.76	0.73	0.77	0.90	0.87	0.85
	D_1	8.1	10.2	10.3	8.2	12.9	9.9	9.9	11.5	10.5	5.4	11.2	10.3	9.3	11.8	10.1	7.5	7.4	8.6
	D_2	17.7	19.6	18.9	18.8	19.1	18.6	18.5	19.1	19.7	17.8	18.0	17.3	18.5	19.4	18.8	16.7	17.1	17.8
PCoA	τ	0.79	0.86	0.81	0.93	0.74	0.83	0.78	0.77	0.85	0.90	0.79	0.88	0.73	0.77	0.81	0.85	0.84	0.82
	D_1	8.5	7.2	8.4	7.0	11.1	8.3	8.8	9.6	7.2	5.8	9.5	8.3	10.6	10.4	8.6	7.7	9.3	8.9
	D_2	17.9	18.7	18.6	18.3	17.3	17.5	18.6	18.1	17.8	18.8	15.8	16.8	18.2	19.2	18.4	17.8	17.9	18.5
LNMDS (1D)	τ	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	D_1	3.3	1.9	2.6	1.9	3.8	1.0	2.8	2.2	2.8	2.6	2.7	2.7	4.2	3.7	3.2	4.2	2.7	1.8
LNMDS (2D)	τ	0.99	0.98	1.00	0.98	0.97	1.00	1.00	1.00	1.00	1.00	0.92	1.00	1.00	0.90	0.99	0.99	0.98	0.99
	D_1	4.3	2.6	3.9	2.8	4.9	3.5	3.4	3.2	3.5	1.8	6.1	5.1	4.1	7.7	3.8	3.0	4.0	2.9
	D_2	7.5	5.6	7.2	9.0	6.9	10.3	7.8	7.2	7.1	13.5	9.5	9.8	7.2	13.1	6.1	12.5	8.4	8.0
GO	τ	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.99	1.00	1.00	1.00	1.00	1.00	0.97	1.00	0.97	1.00	1.00
	D_1	2.4	1.0	1.3	2.8	2.6	2.4	4.5	4.0	2.7	1.2	1.5	1.9	2.6	3.8	3.1	3.7	2.9	3.4

Table 3.3 Ordination performance statistics for experiment 2, in which simulated coenoclines were used to investigate the effects on ordination of variation in the shape of species response curves. All models had a beta diversity of approximately 6 Z and no noise was added.

achieved perfect rank order recovery and LNMDS(1D) improved the fit slightly for replicate 1. On the other hand, the GO ordinations were all inferior in terms of D1 to the DCA solutions, and in two cases rank order recovery was imperfect. This indicates a lack of robustness of GO to consistent skewness of the response curves.

For the models with curves of varying skewness, DCA, LNMDS(1D) and GO each recovered the correct rank order of samples for all replicates. Both LNMDS(1D) and GO achieved a somewhat better fit than DCA for replicate 3. PCA-CS managed perfect rank order recovery on its first axis for two of the replicates, but exhibited considerable involution in the case of the other replicate.

The results from the first four sets of models, each of which had unimodal response curves for all species, may therefore be summarised as follows : DCA produced acceptable results in all cases and LNMDS(1D) and/or GO were sometimes able to improve on these solutions, although GO was sensitive to extreme skewness.

The situation was somewhat different for the two sets of competition models, both of which included some bimodal and multimodal response curves. The only method to achieve perfect rank order recovery for all the competition models was LNMDS(1D). Thus DCA can fail to recover the correct rank order of samples in the presence of non-unimodal response curves. In the case of the competition models with symmetrical physiological response curves, DCA recovered the correct sample order for two of the replicates and GO maintained this order, with a slight improvement in D1. For the other replicate, perfect rank order recovery was only achieved by LNMDS(1D) and,

surprisingly, by PCA-CS.

For the competition models with skewed physiological response curves, DCA achieved perfect recovery of the sample order for only one of the replicates. Both LNMDS(1D) and PCA-CS were successful in this respect for all three replicates. However, the PCA-CS ordinations exhibited strong curvature onto the second axis.

3.3.4 Discussion and Conclusions

Of the methods compared in the present experiment, LNMDS(1D) was the most consistently successful, since it achieved perfect rank order recovery for all models. This indicates that LNMDS has a greater robustness with respect to variation in response curve shape than DCA and GO. Displacement errors (D1) for LNMDS(1D) were either smaller than or not much greater than those for DCA and GO in all cases.

This experiment indicates that DCA is robust to variation in the skewness of unimodal response curves, but that the method can fail to achieve perfect rank order recovery when some non-unimodal curves are included in the model. Nevertheless, the degree of rank order reversal which occurred with some of the competition models in this experiment was far less than that due to the systematic involution of extreme samples in ordinations at this level of beta diversity by PCA-C, PCA-BC or PCoA.

Austin (1976b) reported that involution of extreme samples occurred in Reciprocal Averaging (RA) ordinations of a model coenocline based on beta functions of mixed skewness and a coenocline based on an ecological response model, employing the same type of linear interaction

between species used in the present study. Since the first axis solutions by RA are always monotonic with those produced by DCA, the non-involution of gradient extremes by DCA for models with skewed response curves and competition models in the present experiment would appear to contradict Austin's results. However, a re-examination of Austin's models (Austin 1976a) revealed that they differ from those used in the present study in one important respect: they lack any species with modes located beyond the extremes of the sampled gradient. Austin's ecological response model (Austin 1976a: Figure 4) was therefore subjected to ordination by RA and the set of methods compared in the present study, both in its original form, and with an additional species added at each end of the gradient. The added species had their theoretical modes located outside the extremes of the gradient and the tails of their response curves extended monotonically into the sampled region of the coenocline. Involution of one end of the gradient occurred in both RA and DCA ordinations of the original model. However, both methods recovered the correct rank order of samples after the terminal species were added. This suggests that the involution noted by Austin is a consequence of the lack of any species which reach their maximum abundance at the ends of the gradient, rather than the non-Gaussian response curves.

The models used in the present study, like those of Gauch and Whittaker (1972a, 1976) always include species which attain their maximum abundance at one extreme of the sampled region. Species with these types of distributions appear in most of the published results of direct gradient analyses. However, it is possible to conceive of field situations in which no species reach their maximum value at the extremes

of a gradient. This may occur for gradients which exceed the physiological limits of all species under consideration. One example may be the distribution of species along a moisture gradient extending into conditions of extreme aridity. Beyond the mode of the most drought tolerant or resistant species, the abundances of all species would be expected to decline. The reason for the involution of the extreme samples by DCA and RA under these circumstances can readily be understood in terms of the weighted averages interpretation of the techniques (see Appendix A, section A.4). Sample scores in these methods may be viewed as weighted averages of the scores of the species occurring in them. It is therefore not possible for any samples to be ordinated beyond the estimated modal position of the most extreme species.

GO proved capable of improving on the DCA solutions (in terms of D1) for the symmetrical models and some of the slightly skewed and mixed skewness models. Some improvement in fit also occurred for all of the competition models, although the advantage was generally trivial. Austin (1976b) reported poor results when GO was applied to his ecological response model: the rank order of one sample was altered and the spacing of samples was uneven. Re-examination of the model revealed that the incorrectly placed sample contained only one species. Since only non-zero values are considered when fitting Gaussian regressions, the positions of such samples are ambiguous for GO. They may equally well be placed on either tail of the fitted curve for the species in question. Austin presumably used a random initial configuration and, by chance, the offending sample ended up on the wrong tail. When the model was re-ordinated in the present study, using the (involuted) DCA

solution as an initial configuration, the correct sample order was recovered by GO.

Austin (1976b) suggested that GO was capable of the systematic displacement of samples, in order to "Gaussianise" asymmetrical curves. This contention was not supported in the present study, since D1 values for the competition models were generally lower for GO than for DCA. The poor solution obtained by Austin may be due to the small number of species in his model. With larger numbers of species any attempt to "Gaussianise" the response curves of some species would invariably decrease the fit for other species, hence a kind of averaging effect would be expected to operate.

A surprising feature of the present results was the success of PCA-CS with the competition models derived from skewed physiological response curves. Rank order recovery was perfect for all three replicates and D1 errors were comparable with those for DCA and LNMDS(1D). Reasonable results were occasionally obtained with PCA-CS with some of the other curve shapes. However, the results of experiment 1 indicate that a beta diversity of 6Z represents an upper limit for the successful application of PCA-CS, beyond which involution of gradient extremes will inevitably occur.

3.4 Experiment 3 : The Joint Effects of Response Curve Shape, Quantitative Noise and Qualitative Noise.

3.4.1 Introduction

This experiment was designed to investigate the extent to which the effects of variation in curve shape may be modified by the introduction of quantitative and/or qualitative sampling errors or noise. In particular, it was of interest to note whether the advantage of LNMDS(1D) over DCA, observed with the competition models in the previous experiment, was maintained in the presence of noise.

3.4.2 Methods

The models used were those designated as replicate 1 in each of the six curve shape categories in experiment 2. Each model had a beta diversity of about 6Z. From each of these six models, two additional models were produced by adding quantitative noise at levels of 0.1 and 0.2F. Three further models were also produced in each curve shape category, by introducing qualitative error (using the probability of occurrence profiles for each species), both alone and in combination with each of the two levels of quantitative noise. The modal probabilities (P0) for each species were assigned using the default frequency distribution described in section 2.1.3 (Table 2.1), with all "major" species having P0 values in excess of 0.8. The models were sampled using 40 samples, spaced evenly along the simulated coenocline. Each of the 36 data sets was subjected to ordination by the set of techniques listed in section 2.3 and performance statistics were computed. Ordination plots were prepared and inspected.

3.4.3 Results

The full performance statistics are presented in Tables 3.4 and 3.5. As noted in experiment 2, PCA-C, PCA-BC and PCoA were all consistently afflicted by severe curvilinear distortion of the gradient, leading to involution of the extremes. Hence their results will not be considered further. Similarly, the results of LNMDS in two dimensions will not be discussed in detail. They were generally somewhat inferior to those obtained when one dimension was allowed.

DCA proved robust to the effects of quantitative noise. The noise-induced scatter of samples generally resulted in only slight deterioration in the quality of DCA ordinations, as reflected by decreases in τ and increases in D1. Similar considerations applied to LNMDS(1D), so that the relative efficacy of the two techniques was maintained in the presence of quantitative noise. In particular, the superiority of LNMDS(1D) over DCA was preserved for the competition model derived from skewed physiological response curves, even at a noise level of 0.2F (Table 3.4).

As might be expected in view of its behaviour in experiment 1, GO was more severely affected by quantitative noise than both DCA and LNMDS(1D). With noise levels of 0.2F, rank order recovery by GO, as reflected by τ, was consistently worse than that for DCA and LNMDS(1D) for all curve shapes. The failure of GO with the competition model derived from skewed physiological response curves at a noise level of 0.2F was particularly spectacular (Table 3.4).

The effects of the addition qualitative noise, and its interaction

Ordination Method	Performance Statistic	Without Qualitative (Presence-Absence) Noise																	
		Symmetrical ($\alpha=\gamma=4$)			Slightly Skewed ($\alpha=4,\gamma=2$)			Highly Skewed ($\alpha=4,\gamma=1$)			Mixed Skewness ($\alpha=1\text{-}4,\gamma=1\text{-}4$)			Competition Model with Symmetrical Physiological Curves			Competition Model with Skewed Physiological Curves		
		Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)		
		0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2
DCA	τ	1.00	0.99	0.98	1.00	0.99	0.97	1.00	0.99	0.96	1.00	0.99	0.99	1.00	0.99	0.96	0.98	0.93	0.90
	D_1	3.1	3.1	3.7	1.7	2.1	2.7	3.1	3.3	3.9	1.2	1.5	1.7	3.0	3.2	3.6	5.2	5.9	6.7
	D_2	7.6	5.9	6.1	9.0	8.8	6.2	9.3	9.1	8.6	12.8	11.5	4.9	7.9	8.0	5.9	13.3	13.7	14.4
PCA-C	τ	0.69	0.70	0.72	0.89	0.83	0.85	0.65	0.68	0.66	0.85	0.83	0.80	0.62	0.67	0.68	0.69	0.62	0.49
	D_1	10.7	10.7	10.6	6.8	6.9	7.6	12.7	12.7	13.0	8.3	9.4	9.9	12.7	12.6	13.4	21.4	2.14	21.6
	D_2	18.3	18.6	18.4	16.8	13.4	16.7	19.8	19.7	20.3	18.5	18.7	18.9	18.8	18.2	19.5	21.8	22.0	22.4
PCA-CS	τ	0.97	0.90	0.89	0.98	0.83	0.91	1.00	0.94	0.92	0.64	0.67	0.86	0.88	0.86	0.82	1.00	0.95	0.91
	D_1	5.6	5.9	6.4	9.1	9.7	9.6	6.0	6.2	6.2	15.0	15.6	12.0	8.4	9.4	8.7	3.6	4.4	6.1
	D_2	17.7	17.6	17.3	19.7	18.8	19.2	17.1	17.6	17.6	19.6	19.8	19.4	16.7	17.5	17.9	17.3	18.0	18.5
PCA-BC	τ	0.85	0.80	0.78	0.85	0.84	0.77	0.75	0.72	0.69	0.94	0.92	0.91	0.76	0.68	0.76	0.90	0.88	0.85
	D_1	8.1	9.0	9.2	8.2	8.4	9.8	9.9	10.3	11.0	5.4	4.9	6.1	9.3	10.8	9.7	7.5	7.4	8.3
	D_2	17.7	18.4	17.7	18.8	18.7	19.2	18.5	19.1	19.1	17.8	18.4	18.3	18.5	18.9	19.1	16.7	17.3	17.9
PCoA	τ	0.79	0.81	0.85	0.93	0.93	0.91	0.78	0.79	0.76	0.90	0.89	0.88	0.73	0.74	0.73	0.85	0.80	0.76
	D_1	8.5	8.7	8.3	7.0	6.7	7.2	8.8	8.6	9.3	5.8	6.3	6.3	10.6	10.3	10.6	7.7	8.9	10.1
	D_2	17.9	18.0	17.7	18.3	18.0	18.0	18.6	18.6	18.6	18.8	18.8	18.4	18.2	17.9	18.5	17.8	18.0	18.5
LNMDS (1D)	τ	1.00	0.99	0.97	1.00	0.99	0.98	1.00	0.99	0.96	1.00	0.99	0.99	1.00	0.99	0.96	1.00	0.98	0.93
	D_1	3.3	4.0	4.7	1.9	2.1	3.0	2.8	3.1	4.1	2.6	2.8	2.7	4.2	4.3	4.5	4.2	3.6	4.6
LNMDS (2D)	τ	0.99	0.97	0.94	0.98	0.98	0.97	1.00	0.97	0.94	1.00	0.97	0.97	1.00	0.98	0.86	0.99	0.92	0.81
	D_1	4.3	4.8	5.5	2.8	3.3	3.4	3.4	4.3	5.4	1.8	2.6	2.4	4.1	4.5	7.3	3.0	5.4	8.2
	D_2	7.5	8.2	9.2	9.0	10.1	7.8	7.8	9.3	10.5	13.5	14.2	10.4	7.2	8.3	11.7	12.5	14.1	15.8
GO	τ	1.00	0.98	0.93	1.00	0.98	0.97	0.99	0.97	0.93	1.00	0.99	0.94	1.00	0.98	0.93	0.97	0.93	0.52
	D_1	2.4	3.0	4.4	2.8	4.7	3.2	4.5	5.3	6.2	1.2	3.0	3.7	2.6	3.1	5.1	3.7	5.2	19.9

Table 3.4 Ordination performance statistics for experiment 3, in which simulated coenoclines were used to investigate the joint effects of variation in response curve shape, quantitative noise and qualitative noise on ordination. The results presented are for those models with no qualitative noise introduced. All models had a beta diversity of approximately 6 Z.

Ordination Method	Performance Statistic	With Qualitative (Presence-Absence) Noise																	
		Symmetrical ($\alpha=\gamma=4$)			Slightly Skewed ($\alpha=4,\gamma=2$)			Highly Skewed ($\alpha=4,\gamma=1$)			Mixed Skewness ($\alpha=1\text{-}4,\gamma=1\text{-}4$)			Competition Model with Symmetrical Physiological Curves			Competition Model with Skewed Physiological Curves		
		Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)		
		0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2
DCA	τ	0.93	0.88	0.87	0.90	0.90	0.90	0.93	0.91	0.91	0.95	0.93	0.92	0.95	0.94	0.93	0.74	0.73	0.72
	D_1	5.8	6.3	6.9	8.1	6.2	6.2	5.8	7.6	6.5	3.2	4.7	4.8	5.5	5.6	5.7	10.5	10.9	11.2
	D_2	8.4	8.6	10.2	11.0	12.2	9.5	9.1	10.4	10.2	7.5	8.1	9.0	11.0	10.4	10.3	14.6	15.3	15.0
PCA-C	τ	0.66	0.66	0.72	0.58	0.73	0.71	0.60	0.31	0.65	0.81	0.65	0.64	0.52	0.54	0.54	0.47	0.46	0.44
	D_1	14.9	14.4	13.6	17.5	12.8	13.2	17.2	20.6	16.7	9.4	13.9	14.0	18.6	18.5	18.9	19.5	20.8	22.2
	D_2	20.9	20.4	21.0	21.2	20.2	19.7	21.7	23.4	22.4	18.8	19.6	20.4	21.8	22.0	22.4	22.4	22.9	23.6
PCA-CS	τ	0.79	0.82	0.79	0.77	0.80	0.80	0.86	0.79	0.77	0.86	0.87	0.82	0.81	0.76	0.71	0.89	0.87	0.81
	D_1	9.8	8.7	11.6	12.3	11.0	15.7	8.6	10.6	12.6	12.1	7.5	10.0	10.9	12.3	14.5	7.1	8.0	9.8
	D_2	18.8	19.2	19.7	20.7	20.1	21.8	18.9	19.5	21.0	20.0	19.9	20.2	18.5	19.3	20.7	18.2	18.3	19.1
PCA-BC	τ	0.70	0.69	0.64	0.62	0.51	0.47	0.61	0.58	0.68	0.84	0.80	0.77	0.69	0.67	0.64	0.70	0.71	0.69
	D_1	12.1	13.4	14.3	15.1	19.6	19.4	14.2	15.1	13.3	7.6	8.8	10.8	10.8	12.0	13.5	10.7	10.9	11.5
	D_2	20.1	20.6	20.4	20.3	20.0	21.0	20.5	21.6	20.9	19.0	19.7	19.9	19.6	19.9	20.6	17.6	18.3	19.0
PCoA	τ	0.74	0.75	0.75	0.59	0.76	0.70	0.66	0.56	0.64	0.84	0.76	0.77	0.62	0.65	0.67	0.63	0.62	0.60
	D_1	11.0	11.1	10.3	17.4	11.3	13.9	12.2	16.4	12.3	7.5	10.8	11.0	13.5	13.1	13.3	12.4	12.8	13.2
	D_2	20.3	19.1	19.8	21.1	20.3	20.2	20.3	21.7	20.9	18.5	19.2	20.0	19.3	19.3	19.7	18.5	19.0	19.7
LNMDS (1D)	τ	0.92	0.84	0.82	0.86	0.86	0.89	0.91	0.84	0.90	0.95	0.91	0.89	0.93	0.92	0.91	0.69	0.68	0.68
	D_1	6.2	8.1	8.1	11.1	9.3	7.9	6.1	11.1	7.0	4.3	5.7	6.1	7.5	7.9	8.0	11.6	12.7	13.2
LNMDS (2D)	τ	0.89	0.86	0.86	0.87	0.89	0.88	0.90	0.81	0.89	0.94	0.87	0.86	0.90	0.90	0.92	0.68	0.67	0.68
	D_1	7.5	7.8	6.3	10.1	7.4	8.1	6.0	11.3	6.8	4.1	7.9	7.7	8.0	8.0	7.6	11.4	12.5	13.0
	D_2	15.7	13.7	12.8	14.7	16.1	11.0	11.0	16.5	12.5	9.9	17.0	17.9	13.9	13.9	13.8	16.4	17.2	17.7
GO	τ	0.96	0.94	0.91	0.92	0.96	0.89	0.99	0.96	0.92	0.99	0.95	0.86	0.99	0.95	0.88	0.72	0.65	0.58
	D_1	4.6	4.0	4.9	7.0	3.8	5.6	4.8	6.7	6.7	1.8	3.4	7.9	4.5	6.1	10.3	16.8	17.0	19.0

Table 3.5 Ordination performance statistics for experiment 3, in which simulated coenoclines were used to investigate the joint effects of variation in response curve shape, quantitative noise and qualitative noise on ordination. The results presented are for those models with qualitative noise added. All models had a beta diversity of approximately 6 Z.

with quantitative noise, were similar for all models, with the exception of the competition model with skewed physiological response curves. In the presence of qualitative noise only, or qualitative noise accompanied by quantitative noise at a level of 0.1F, the results of GO were consistently superior to those of DCA which, in turn, were better than those of LNMDS(1D) (Table 3.5). The relative robustness of GO to the introduction of qualitative noise was noted previously in discussing the results of experiment 1. It is probably due to the disregarding of zero values when fitting the Gaussian regressions for species abundances in GO. However, the advantage of GO over DCA disappeared when quantitative noise at a level of 0.2F was applied in addition to qualitative noise.

In the case of the competition model derived from skewed physiological response curves, the effects of qualitative noise, with or without quantitative noise, were relatively severe for all methods. GO was inferior to DCA and LNMDS(1D), even without quantitative noise. The best results for this model, in the presence of qualitative noise, were obtained by PCA-CS. The superiority of LNMDS(1D) over DCA for this model, noted in the absence of qualitative noise, was not maintained after the addition of qualitative noise (Table 3.5).

3.4.4 Conclusions

The results of this experiment suggest that the greater robustness of LNMDS(1D), as compared with DCA, to variation in response curve shape is maintained in the presence of quantitative sampling errors. However, the addition of qualitative noise appears to favour DCA over LNMDS(1D). The performance of GO is adversely affected by quantitative noise, but the method appears less sensitive to qualitative errors than both DCA

and LNMDS(1D). Further research is necessary to establish the relative importance of quantitative and qualitative noise in vegetation data.

3.5 Experiment 4 : The Effects of Sample Distribution Along 6Z Coenoclines

3.5.1 Introduction

All experiments described thus far have used samples spaced evenly over the entire length of the simulated coenoclines. It is extremely unlikely that such an even distribution of samples along a single underlying gradient would be attained in a real vegetation study. Usually, sites representing certain levels of the gradient would be more frequently represented in a landscape than others, so that samples may be concentrated in some parts of a gradient even if sampling of the landscape is equitable on an areal basis (e.g. Goodall 1954a). If the identity of the underlying gradient is apparent prior to sampling, the stratification of sampling with respect to some index of position along the gradient may ensure a more even distribution of samples along the gradient. However, the resulting arrangement is unlikely to be completely regular.

This experiment was designed to examine the effects of various sampling arrangements on the performance of ordination methods.

3.5.2 Methods

Four coenocline models, all with beta diversities of about 6Z were used. These were :

(1) a model with symmetrical, unimodal response curves ($\alpha=\gamma=4$),

(2) a model with highly skewed, unimodal curves ($\alpha=4,\gamma=1$),

(3) a competition model derived from symmetrical physiological response curves and

(4) a competition model derived from skewed physiological response curves.

They are the same models designated as replicate number 1 in their respective curve shape categories in experiment 2. Ordination results for evenly spaced samples were thus already available. Three additional sampling patterns were produced as follows :

(1) A total of 40 samples were placed at random along the coenocline.

(2) The coenocline was divided into 10 segments of equal length and samples were placed randomly within each segment in the ratio 2:2:4:4:8:8:4:4:2:2, the total number of samples being 40. This arrangement favours the central region of the gradient.

(3) The coenocline was divided into 10 segments of equal length and samples were placed randomly within each segment in the ratio 7:5:3:3:2:2:3:3:5:7, the total number of samples again being 40. The extremes of the gradient are favoured in this pattern.

The distribution of the samples in each of these arrangements is illustrated in Figure 3.7.

Each coenocline model was sampled using each of the sampling patterns, producing a total of 16 data sets, including those sampled

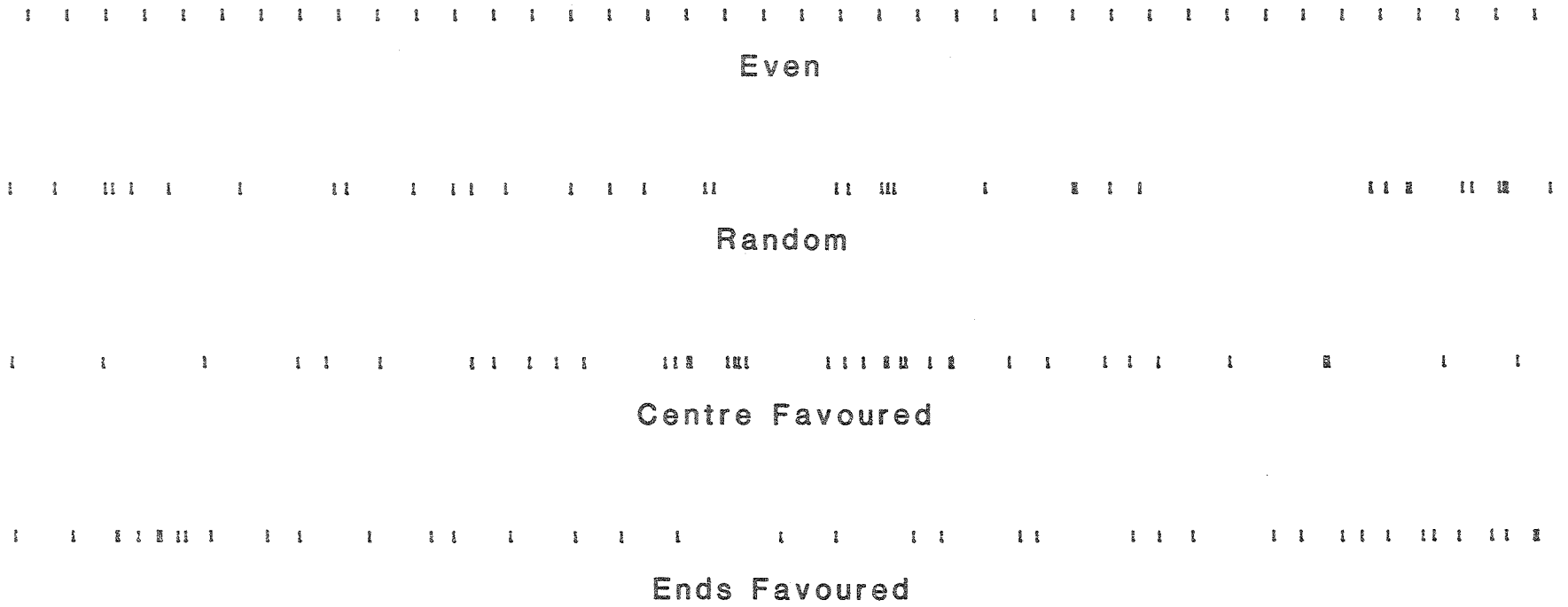


Figure 3.7 The four sampling arrangements used in experiment 4. Each dash indicates the position of a sample along the model coenocline axis.

with an even arrangement. These data sets were subjected to ordination by each of the techniques compared in previous experiments and performance statistics were computed. Plots of the ordination configurations were prepared and inspected.

3.5.3 Results

Performance statistics are given in Table 3.6. With symmetrical, unimodal response curves DCA, LNMDS(1D) and GO all displayed little variation in performance between different sampling arrangements. Each of the three methods achieved perfect rank order recovery in all cases and displacement errors (D1) did not differ greatly between sampling patterns. GO maintained a consistent marginal advantage (in terms of D1), over DCA. LNMDS(1D) ordinations were all slightly worse than the DCA ordinations in this respect.

For PCA-C, PCA-BC and PCoA, all of which were subject to involution, the observed differences in performance (especially in terms of τ) can be attributed to the occurrence of greater or lesser numbers of samples towards the involuted extremes of the gradient. Thus rank correlations for these methods are generally lowest for either the sampling pattern favouring the ends of the gradient or the random pattern, which had a clump of samples near one end of the gradient (Figure 3.7). In the case of PCA-CS, rank order recovery failed for the even sample arrangement and that favouring the ends due to a slight concavity of one flank of the arch configuration on the first two axes. Both random sampling and sampling favouring the centre of the gradient resulted in perfect rank order recovery, since they placed no samples in this critical region.

Ordination Method	Performance Statistic	Symmetrical (α=γ=4)				Highly Skewed (α=4,γ=1)				Competition Model with Symmetrical Physiological Curves				Competition Model with Skewed Physiological Curves			
		Sample Arrangement				Sample Arrangement				Sample Arrangement				Sample Arrangement			
		Even	Random	Centre	Ends	Even	Random	Centre	Ends	Even	Random	Centre	Ends	Even	Random	Centre	Ends
DCA	τ	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	0.97	1.00
	D_1	3.1	3.0	3.0	3.0	3.1	3.5	2.9	3.4	3.0	2.8	3.6	3.5	5.2	2.3	4.7	3.8
	D_2	7.6	8.2	6.4	7.1	9.3	9.1	8.8	8.5	7.9	7.9	7.1	9.1	13.3	9.3	10.9	14.1
PCA-C	τ	0.69	0.67	0.75	0.56	0.65	0.81	0.68	0.62	0.62	0.88	0.49	0.54	0.69	0.26	0.77	0.61
	D_1	10.7	10.1	12.2	9.9	12.7	11.4	14.3	10.7	12.7	9.5	15.0	10.0	21.4	31.1	16.9	22.4
	D_2	18.3	20.2	16.0	19.0	19.8	21.7	17.0	20.8	18.8	20.8	16.9	19.6	21.8	24.0	18.5	23.8
PCA-CS	τ	0.97	1.00	1.00	0.97	1.00	1.00	1.00	1.00	0.83	0.80	0.95	0.78	1.00	1.00	1.00	1.00
	D_1	5.6	5.3	5.2	5.5	6.0	6.2	6.2	5.1	8.4	9.8	7.9	8.7	3.6	5.4	3.8	3.3
	D_2	17.7	19.6	14.6	19.8	17.1	19.0	14.3	19.1	16.7	18.9	14.0	18.5	17.3	18.9	14.5	19.2
PCA-BC	τ	0.85	0.78	0.93	0.74	0.75	0.75	0.88	0.64	0.76	0.82	0.78	0.81	0.90	0.87	0.94	0.86
	D_1	8.1	7.9	8.5	7.5	9.9	9.7	9.8	8.5	9.3	8.5	11.6	6.7	7.5	9.7	8.5	6.2
	D_2	17.7	19.4	15.4	18.6	18.5	20.4	16.1	19.5	18.5	20.1	16.6	19.2	16.7	18.1	14.6	17.8
PCoA	τ	0.79	0.76	0.86	0.79	0.78	0.77	0.90	0.77	0.73	0.80	0.69	0.74	0.85	0.92	0.87	0.90
	D_1	8.5	7.8	10.1	7.1	8.8	10.0	9.0	6.4	10.6	7.5	12.9	8.0	7.7	8.1	10.9	3.2
	D_2	17.9	19.6	16.1	18.5	18.6	20.2	16.4	19.6	18.2	19.8	16.6	18.6	17.8	19.3	16.2	19.0
LNMDS (1D)	τ	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	D_1	3.3	3.9	3.1	3.2	2.8	2.9	2.8	2.9	4.2	4.9	3.8	4.3	4.2	4.3	3.5	4.2
LNMDS (2D)	τ	0.99	0.97	0.99	0.96	1.00	1.00	1.00	1.00	1.00	0.99	1.00	0.97	0.99	0.96	1.00	0.96
	D_1	4.3	4.9	3.9	4.3	3.4	3.5	3.5	3.6	4.1	4.0	3.8	4.7	3.0	3.7	3.7	2.2
	D_2	7.5	8.4	5.7	7.1	7.8	7.9	7.4	7.5	7.2	7.2	6.8	8.0	12.5	10.4	10.4	13.1
GO	τ	1.00	1.00	1.00	1.00	0.99	1.00	1.00	0.99	1.00	1.00	1.00	1.00	0.97	1.00	0.91	1.00
	D_1	2.4	2.6	2.0	2.6	4.5	4.8	3.3	4.5	2.6	2.6	3.2	2.4	3.7	2.1	10.3	2.4

Table 3.6 Ordination performance statistics for experiment 4, in which simulated coenoclines were used to assess the joint effects of variation in response curve shape and the arrangement of samples on ordination. All models had a beta diversity of approximately 6Z and no noise was added.

For the highly skewed model, little variation in the performance of DCA, LNMDS(1D), GO and PCA-CS with different sampling arrangements was noted. DCA, LNMDS(1D) and PCA-CS always achieved perfect rank order recovery and the accuracy of sample position recovery (as reflected by D1) varied from best to worst in the order LNMDS(1D) > DCA > GO > PCA-CS.

With the competition model derived from symmetrical response curves, no marked variation in the performance of DCA, LNMDS(1D) and GO with sampling pattern was apparent. All three methods consistently achieved perfect rank order recovery, with the same relative accuracy (in terms of D1) as for the symmetrical model (i.e. GO > DCA > LNMDS(1D)). PCA-CS consistently failed to recover the correct rank order of samples for this model.

In the case of the competition model derived from skewed physiological response curves, the situation was more complex. LNMDS(1D) displayed consistent success, with perfect rank order recovery in all cases and little variation in D1. For DCA, variation in performance between sampling arrangements was more marked than that observed for the other three models. Perfect rank order recovery was achieved for the random pattern and the arrangement favouring the ends of the gradient, but not for the other two patterns. It appears that the success of DCA with this type of model depends on the occurrence or otherwise of samples in certain critical segments of the coenocline, where the bimodality of the response curves of some species may cause the local reversal of sample sequences. GO also exhibited considerable variation in performance between sampling patterns with this model. Its

performance was particularly poor with the arrangement favouring the centre of the gradient. The somewhat surprising success of PCA-CS with this model, noted in experiment 3, was maintained between different sampling patterns.

3.5.4 Conclusions

In most cases, the effects of different sampling patterns on the performance of DCA, LNMDS(1D) and GO appear to be small, and the relative success of these methods remains constant between sampling patterns.

Mohler (1981) reported that DCA tended to recover sample positions along in a simulated Gaussian coenocline with a beta diversity of about 4Z more accurately when samples were clustered towards the extremes of the gradient. The present results do not support this observation. The performance of DCA with the symmetrical model in the present study was remarkably uniform between different sampling patterns. Mohler's conclusion is based on the more accurate recovery of relative sample positions for sampling patterns in which nearly all samples were placed at, or very near the extremes of the gradient. These arrangements were more extreme than that used in the present study. To claim greater accuracy of recovery of sample positions with such extreme sampling patterns is misleading. In the limiting case, if half the samples were placed at one end of the gradient and half at the other end, all ordinations (in the absence of sampling error) would consist of two points, with half the samples located at each. The accuracy of recovery of sample locations would presumably be considered "perfect".

The results of the present experiment do not support Mohler's

recommendation, that field sampling should attempt to favour the extremes of perceived gradients. A sampling approach which endeavours to spread samples fairly evenly over the underlying gradients seems preferable (see section 4.5.4).

3.6 Experiment 5 : The Effects of Carrying Capacity Variation

3.6.1 Introduction

The results of direct gradient analyses have often revealed systematic variations in biomass (or standing crop) along environmental gradients. For example, the data of Whittaker and Niering (1975) shows a monotonic increase in biomass with elevation. In vegetation studies where the abundances of species in samples have been recorded using some appropriate measure (e.g. percentage canopy cover, stem density), the total of the abundance measures for all species present in a sample (=stand abundance of Austin 1981) may be regarded as a crude index of standing crop. Hence stand abundance may be expected to vary systematically along environmental gradients under some circumstances.

In the models used in the experiments described thus far, no attempt was made to control the variation of stand abundance along the simulated coenoclines. Examination of the behaviour of stand abundance along the gradients in these models generally revealed no tendency for systematic variation. Normally, stand abundance exhibited irregular oscillations along the gradient, with local peaks co-inciding with the modes of major species.

This experiment examines the effects on ordinations of introducing systematic variation in stand abundance along simulated coenoclines. In

non-seral vegetation, stand abundance may be regarded as a reflection of "environmental carrying capacity". Hence the expression "carrying capacity adjustments" will be used here to describe the process of controlling the variation in stand abundance along the artificial gradients.

3.6.2 Methods

The effects of carrying capacity adjustments were investigated using the same four models employed in experiment 4 (see section 3.5.2). Two types of carrying capacity adjustment were studied. In the first, stand abundances were made to vary linearly along the coenocline, with the stand abundance at one end of the simulated gradient being half that at the other end. In the second approach, the relationship between stand abundance and the coenocline was parabolic, with stand abundances at both ends of the gradient being half that at the centre of the gradient (cf. Austin 1976a). Data sets incorporating each of these adjustments were derived for each of the four models. In each case, 40 evenly spaced samples were used. The data sets were subjected to ordination by the set of techniques listed in section 2.3 and performance statistics were computed.

Carrying capacity adjustments tend to alter the shapes of the response curves for individual species. Figure 3.8 illustrates the form of species response profiles in the "symmetrical" and "highly skewed" models after linear and parabolic adjustments were performed. These may be compared with original models, illustrated in Figure 3.6. Note that symmetrical, bell-shaped response curves may become skewed or shouldered after carrying capacity adjustments.

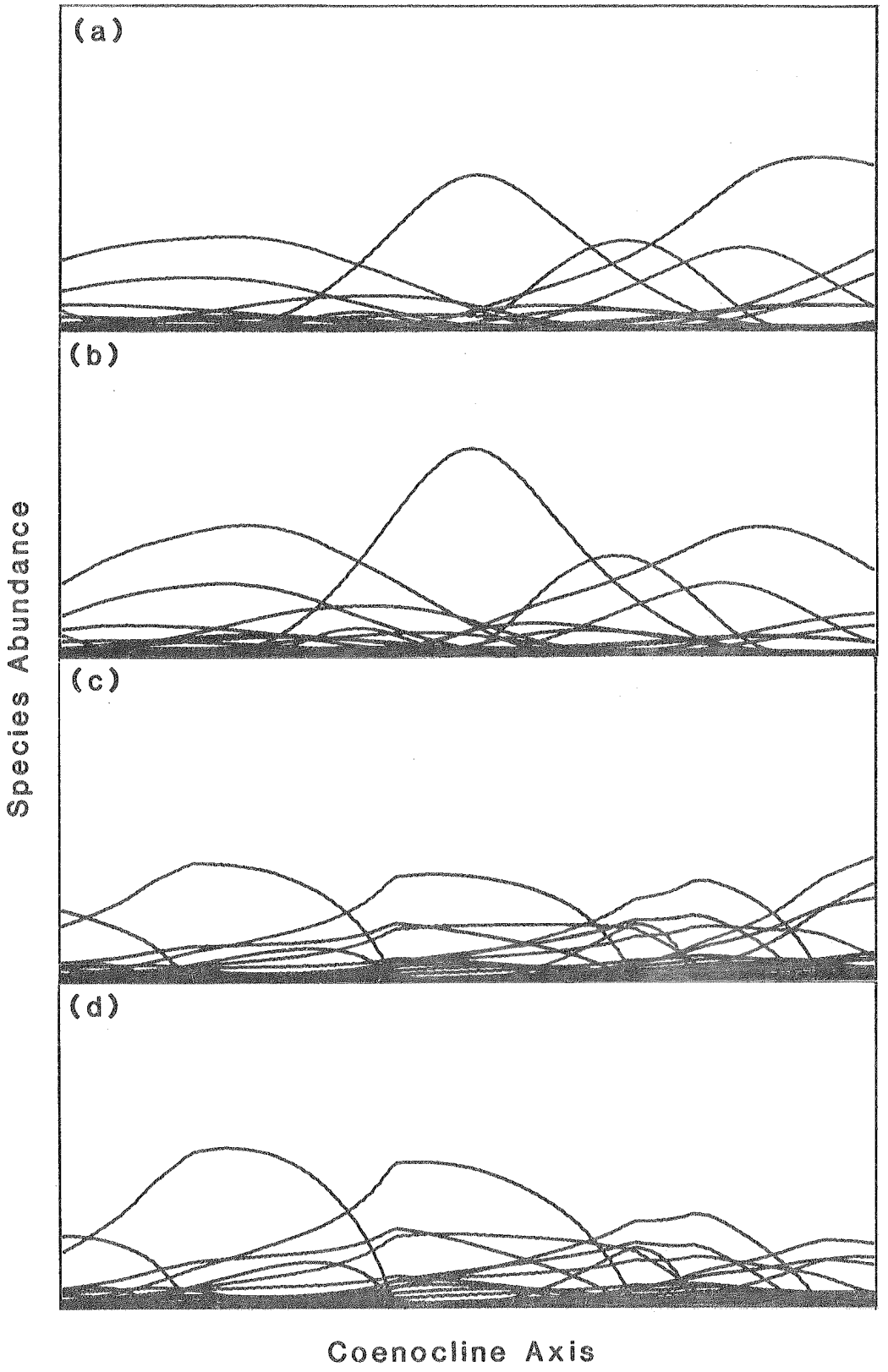


Figure 3.8 An illustration of the effects of carrying capacity adjustments on the shape of species response curves. In coenoclines (a) and (c) stand abundance (i.e. the total of the abundances of all species present in a sample) increases linearly from left to right, with the stand abundance at the extreme right being twice that at the extreme left. In coenoclines (b) and (d) stand abundance varies quadratically along the coenocline, with the value at the midpoint being twice that at both extremes. In (a) and (b) the adjustments have been applied to the same symmetrical model previously illustrated in Figure 3.6(a), while (c) and (d) refer to the highly skewed model shown in Figure 3.6(c).

3.6.3 Results

Performance statistics are presented in Table 3.7. The relative order of performance of DCA, LNMDS(1D) and GO (the most successful techniques with the original models) was not significantly altered by either of the carrying capacity adjustments. With the data sets derived from the symmetrical model, all three techniques still achieved perfect rank order recovery after both adjustments. LNMDS(1D) solutions were consistently somewhat inferior to those of DCA. In both cases, the accuracy of the recovery of sample positions was slightly better for GO compared with DCA. However, the advantage of GO over DCA was reduced by the carrying capacity adjustments. This is most probably attributable to the slight asymmetry of response curves after adjustment (Figure 3.8), which conflicts with the Gaussian model of GO. Among the other techniques, PCA-CS was able to achieve perfect rank order recovery and a lower value of D1 than DCA, for the symmetrical model with linear variation in stand abundance.

For the data sets derived from the highly skewed model, DCA and LNMDS(1D) both maintained perfect rank order recovery after both carrying capacity adjustments. D1 values for LNMDS(1D) were consistently less than those for DCA. The failure of GO to preserve the correct rank order of samples with the original model (section 3.3.3) persisted after both adjustments.

For the competition model derived from symmetrical physiological response curves, perfect rank order recovery by DCA, LNMDS(1D) and GO was maintained after both carrying capacity adjustments. The relative

Ordination Method	Performance Statistic	Symmetrical ($\alpha=\gamma=4$) Carrying Capacity None	Symmetrical ($\alpha=\gamma=4$) Carrying Capacity Linear	Symmetrical ($\alpha=\gamma=4$) Carrying Capacity Adjustment Parabolic	Highly Skewed ($\alpha=4,\gamma=1$) Carrying Capacity None	Highly Skewed ($\alpha=4,\gamma=1$) Carrying Capacity Linear	Highly Skewed ($\alpha=4,\gamma=1$) Carrying Capacity Adjustment Parabolic	Competition Model with Symmetrical Physiological Curves Carrying Capacity None	Competition Model with Symmetrical Physiological Curves Carrying Capacity Linear	Competition Model with Symmetrical Physiological Curves Carrying Capacity Adjustment Parabolic	Competition Model with Skewed Physiological Curves Carrying Capacity None	Competition Model with Skewed Physiological Curves Carrying Capacity Linear	Competition Model with Skewed Physiological Curves Carrying Capacity Adjustment Parabolic
DCA	τ	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.99	0.98
	D_1	3.1	3.0	3.1	3.1	3.3	3.1	3.0	2.6	3.2	5.2	3.9	5.2
	D_2	7.6	7.1	7.6	9.3	9.0	9.3	7.9	7.9	8.1	13.3	12.9	13.3
PCA-C	τ	0.69	0.77	0.62	0.65	0.81	0.63	0.62	0.74	0.48	0.69	1.00	0.34
	D_1	10.7	11.1	12.8	12.7	10.7	14.5	12.7	9.7	18.6	21.4	8.7	21.3
	D_2	18.3	18.4	21.3	19.3	19.5	21.8	18.8	17.5	21.8	21.8	20.6	24.1
PCA-CS	τ	0.97	1.00	0.97	1.00	1.00	0.97	0.88	0.90	0.81	1.00	1.00	0.93
	D_1	5.6	3.7	7.0	6.0	9.0	7.2	8.4	7.3	9.6	3.6	8.6	7.0
	D_2	17.7	17.5	18.2	17.1	17.3	17.3	16.7	16.6	17.4	17.3	17.6	18.2
PCA-BC	τ	0.85	0.82	0.82	0.75	0.73	0.75	0.76	0.76	0.81	0.90	0.88	0.91
	D_1	8.1	9.2	9.2	9.9	10.8	10.6	9.3	9.4	8.4	7.5	7.4	6.4
	D_2	17.7	17.5	17.3	18.5	19.7	19.2	18.5	18.5	18.4	16.7	17.7	17.1
PCoA	τ	0.79	0.80	0.79	0.78	0.77	0.77	0.73	0.75	0.72	0.85	0.90	0.83
	D_1	8.5	8.7	9.1	8.8	9.1	9.1	10.6	10.1	11.0	7.7	6.4	8.3
	D_2	17.9	18.0	17.8	18.5	19.0	18.9	18.2	18.2	18.2	17.8	17.9	18.2
LNMDS (1D)	τ	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	D_1	3.3	3.6	3.6	2.8	3.0	2.5	4.2	3.6	4.3	4.2	5.6	3.0
LNMDS (2D)	τ	0.99	0.97	0.95	1.00	1.00	0.99	1.00	0.99	0.94	0.99	0.99	0.99
	D_1	4.3	4.6	4.9	3.4	3.4	3.5	4.1	3.3	5.5	3.0	2.4	3.8
	D_2	7.5	7.2	7.9	7.8	7.3	9.0	7.2	7.4	8.8	12.5	12.2	12.7
GO	τ	1.00	1.00	1.00	0.99	0.99	0.99	1.00	1.00	1.00	0.97	0.99	0.97
	D_1	2.4	2.8	2.8	4.6	5.1	5.1	2.6	2.3	2.1	3.7	2.5	4.9

Table 3.7 Ordination performance statistics for experiment 5, in which simulated coenoclines were used to study the effects on ordination of variation in response curve shape and carrying capacity adjustments. All models had a beta diversity of approximately 6Z and no noise was added.

accuracy of sample position recovery remained in the order (from best to worst) GO > DCA > LNMDS(1D).

With the competition model derived from skewed physiological response curves, variation in the performance of individual methods with different carrying capacity adjustments was greater than that observed for the other three models. LNMDS(1D) was the only technique which consistently achieved perfect rank order recovery. With parabolic variation in carrying capacity, it also obtained the smallest value of D1. On the other hand, in the presence of linear variation in stand abundance, D1 values for both DCA and GO were considerably less than those for LNMDS(1D). However, neither DCA nor GO achieved perfect rank order recovery in this case.

3.6.4 Conclusions

The effect of systematic variations in stand abundance along coenoclines, on the performance of those ordination methods which have proved most successful in previous experiments, is relatively minor. DCA, LNMDS(1D) and GO all appear to be reasonably robust to such variation. Some changes in the relative performance of the methods were noted after carrying capacity adjustments. However, these were generally marginal. Further experiments on the effects of systematic variation in stand abundance on ordinations are necessary.

3.7 General Conclusions

The present experiments with simulated coenoclines suggest the following major conclusions :

(1) For coenoclines in which response curves are unimodal, DCA is generally the most successful of the techniques compared. GO can improve significantly on DCA solutions only when the response curves are fairly symmetrical, beta diversity is less than about 6Z and quantitative noise levels are low.

(2) When some species have bimodal or multimodal response curves (due to interspecific competition) LNMDS with the percentage similarity coefficient produces better results than both DCA and GO, provided that the ordination is performed in one dimension.

(3) PCoA (with percentage similarity) and PCA-C are ineffective for ecological ordination of coenoclines unless the beta diversity is less than about 3Z. Of the PCA variants examined, PCA-CS is the least affected by curvilinear distortion at a given beta diversity. However, it tends to represent samples near the ends of coenoclines as relative outliers.

(4) The distribution of samples along coenoclines does not appear to have serious effects on the accuracy of the recovery of sample positions by DCA, GO or LNMDS. There is no evidence that concentration of samples towards the ends of gradients improves the performance of these methods.

(5) DCA, GO and LNMDS are all relatively robust to twofold variations in stand abundance along coenoclines.

(6) Two situations have been identified in which DCA (and RA) can fail

to recover the correct rank order of samples along a coenocline, even in the absence of noise. This may occur if (a) some species have multimodal response curves or (b) there is a lack of species which attain their maximum abundance at the ends of the coenocline. In the first case, local reversals of sample order occur. The second situation leads to the involution of extreme samples.

CHAPTER 4 : EXPERIMENTS WITH SIMULATED COENOPLANES

4.1 Introduction

In most field studies, the compositional variation in the vegetation is likely to be related to more than one underlying gradient. Where there are k such gradients, the success of an ordination (for the purpose of indirect gradient analysis) is expressed by the degree to which the trends in compositional variation related to the underlying gradients are clearly and simply represented on the first k ordination axes. The experiments reported in this chapter are based on an extension of the coenocline modelling approach, to produce two-dimensional patterns of compositional variation or coenoplanes. A number of previous studies have employed coenoplane models in which species response surfaces were of Gaussian form (e.g. Austin and Noy-Meir 1971; Gauch, Whittaker and Wentworth 1977; Gauch, Whittaker and Singer 1981). In the present experiments, the effects of variation in the shapes of response surfaces on the performance of ordination methods is studied.

The set of ordination techniques compared in these experiments differed from those used on the coenocline models in two respects. Firstly, GO was not used with the two-dimensional models since it is only appropriate when there is a single underlying gradient. Secondly, LNMDS ordinations were performed in both two and three dimensions, rather than the one and two dimensions used for the coenocline models.

In assessing the accuracy of ordination results for the two-dimensional models, rank correlation coefficients could not be used,

since the concept of rank order has no simple analogue in more than one dimension. Hence ordination performance for the two-dimensional models was assessed soley by means of RMS displacement errors. These were computed for both two- and three-dimensional ordination configurations.

4.2 Experiment 6 : The Joint Effects of the Beta Diversities of Coenoplane Axes, Quantitative Noise and Qualitative Noise with Symmetrical Response Surfaces

4.2.1 Introduction

This experiment investigates the joint effects on ordinations of variation in the absolute and relative beta diversities of coenoplane axes, the introduction of quantitative sampling errors or noise and the introduction of qualitative or presence-absence noise. The response surfaces in all models used on this experiment were unimodal and symmetrical, with powers α and γ on both axes of the coenoplanes being set at 4.0 for all species. As explained in section 3.2.1, beta functions with these powers are very similar in shape to the Gaussian curve. Hence the models used in this experiment allow the present results to be compared, where appropriate, with those of previous studies employing Gaussian models.

4.2.2 Methods

Three coenoplanes were simulated, with beta diversities of 2 X 2Z, 6 X 2Z and 6 X 6Z. In each case, the first figure gives the beta diversity along the X axis of the coenoplane and the second is the beta diversity along the Y axis. Other parameters of the response surfaces were allocated for each coenoplane as follows :

(1) The standard deviation of the ranges of species abundance surfaces

was set at 0.3 times the average value on both axes.

(2) Modal abundances (AO) were allocated randomly from a lograndom distribution, on the range 1 to 100.

(3) Modal probabilities of occurrence (PO) were assigned using the default frequency distribution described in section 2.1.3 (Table 2.1). All "major" species (see below) were given a modal probability of at least 0.8.

(4) No segmentation of either coenoplane axis was performed for the purpose of allocating the positions of species modes. Hence species richness (alpha diversity) does not vary systematically across the coenoplane in these models.

(5) Those 15% of species with the highest abundance surface integrals were designated as "major" and the positions of the modes of major species were adjusted to ensure equitable spacing (see section 2.1.3).

(6) The powers α and γ on both X and Y axes were set at 4.0 for all species. This produces symmetrical, bell-shaped response surfaces.

(7) Rotation angles (θ) for the response surfaces were set at zero for all species.

The total number of species in each case was selected by trial and error, in order to produce an average number of species per sample (alpha diversity) of about 25 for each noiseless model. From each model, six data sets were produced. These represented all factorial combinations of three levels of quantitative noise (0.0,0.1 and 0.2F) and the introduction or otherwise of qualitative noise (using the probability of occurrence surfaces). The 2 X 2Z and 6 X 6Z models were sampled using 49 samples arranged on a regular 7 X 7 grid. In view of

the difference in beta diversity between its X and Y axes, the 6 X 2Z model was sampled using 48 samples on a regular 12 X 4 grid, thus relating the intensity of sampling to the beta diversity on each axis.

The resulting 16 data sets were subjected to ordination by each method. Performance statistics D2 and D3 were computed for each ordination, as described in section 2.2. In the case of the 6 X 2Z models, the definition of the "true" configuration for Procrustean analysis necessitated rescaling of the co-ordinates of samples on the Y axis of the coenoplane, such that their range relative to the X axis co-ordinates reflected the difference in beta diversity. Scatter diagrams of the sample positions on the first two ordination axes were prepared and inspected.

4.2.3 Results

The performance statistics are given in Table 4.1. Interpretation of the values of D2 and D3 should take into account the distance between adjacent samples along each row and column of the sampling grids. This distance was 14.3 units for the 2 X 2Z and 6 X 6Z models and 8.3 units for the 6 X 2Z models. Two-dimensional sample ordinations produced by DCA and LNMDS(2D) for each of the three "noiseless" data sets are presented in Figure 4.1. For PCA-C, PCA-CS and PCoA, sample positions on the first two ordination axes for the noiseless 2 X 2Z and 6 X 6Z models are shown in Figure 4.2. The configurations on both axes 1 v. 2 and 1 v. 3, for ordinations of the noiseless 6 X 2Z data set by these methods, are illustrated in Figure 4.3. In Figures 4.1 to 4.3, samples occurring at the same position along the Y axis of the coenoplane are joined by a line, to facilitate the visualisation of any distortion of

Ordination Method	Performance Statistic	Without Qualitative (Presence-Absence) Noise									With Qualitative (Presence-Absence) Noise								
		Beta Diversity 2 x 2 Z			Beta Diversity 6 x 2 Z			Beta Diversity 6 x 6 Z			Beta Diversity 2 x 2 Z			Beta Diversity 6 x 2 Z			Beta Diversity 6 x 6 Z		
		Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)			Noise Level (F)		
		0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.1	0.2
DCA	D_2	9.4	11.7	13.6	6.3	6.4	6.4	9.8	9.4	10.4	29.7	24.9	34.2	11.6	13.2	13.6	19.5	16.6	15.0
	D_3	13.7	15.0	17.3	8.4	8.4	9.3	14.5	13.2	14.7	31.2	28.2	35.4	13.4	14.7	14.6	21.8	20.8	16.1
PCA-C	D_2	17.9	19.2	22.7	20.4	20.4	20.6	33.9	33.8	33.7	30.5	28.1	30.7	24.5	23.9	23.1	36.1	37.0	35.2
	D_3	19.9	21.8	25.6	20.3	20.1	20.2	34.8	34.6	34.2	31.7	29.7	32.3	25.2	24.6	23.6	36.9	37.6	36.4
PCA-CS	D_2	9.2	12.6	20.2	18.7	18.6	20.7	21.0	20.3	18.4	18.9	22.7	30.4	19.9	20.5	20.2	25.9	27.5	31.1
	D_3	18.8	20.0	25.3	19.9	20.1	20.5	25.8	25.1	24.8	25.1	27.6	32.1	22.5	22.9	22.4	29.8	30.6	32.9
PCA-BC	D_2	12.0	14.1	15.8	21.9	22.6	21.4	20.7	22.1	23.0	26.5	26.1	30.7	23.8	26.2	23.2	25.4	32.3	31.9
	D_3	19.2	19.6	21.7	20.7	21.0	21.0	26.0	26.4	26.4	29.3	31.1	33.0	24.9	26.0	23.2	29.4	33.2	33.2
PCoA	D_2	11.2	13.3	14.3	20.4	20.4	20.3	20.1	20.6	20.7	31.4	26.4	28.6	23.7	23.5	22.2	26.9	29.4	27.1
	D_3	19.6	20.1	20.6	19.8	19.5	19.7	26.0	26.1	26.5	30.2	29.5	31.4	24.3	24.0	21.8	28.3	30.2	31.1
LNMDS (2D)	D_2	8.7	11.3	13.1	4.3	4.2	12.2	6.4	6.7	8.6	25.6	26.5	33.0	18.5	15.4	15.5	11.8	14.0	18.4
LNMDS (3D)	D_2	9.2	11.8	13.4	5.3	4.7	13.9	8.5	9.4	10.5	24.4	24.8	31.8	18.7	16.1	16.3	12.6	18.1	16.6
	D_3	11.8	14.9	18.6	7.6	9.4	12.4	16.3	17.5	18.1	28.3	28.7	33.8	19.8	17.5	18.0	19.3	23.4	21.9

Table 4.1 Ordination performance statistics for experiment 6, in which simulated coenoplanes were used to study the joint effects on ordination of the relative and absolute beta diversities of coenoplane axes, quantitative noise and qualitative noise. Species in all models had symmetrical, bell-shaped response surfaces.

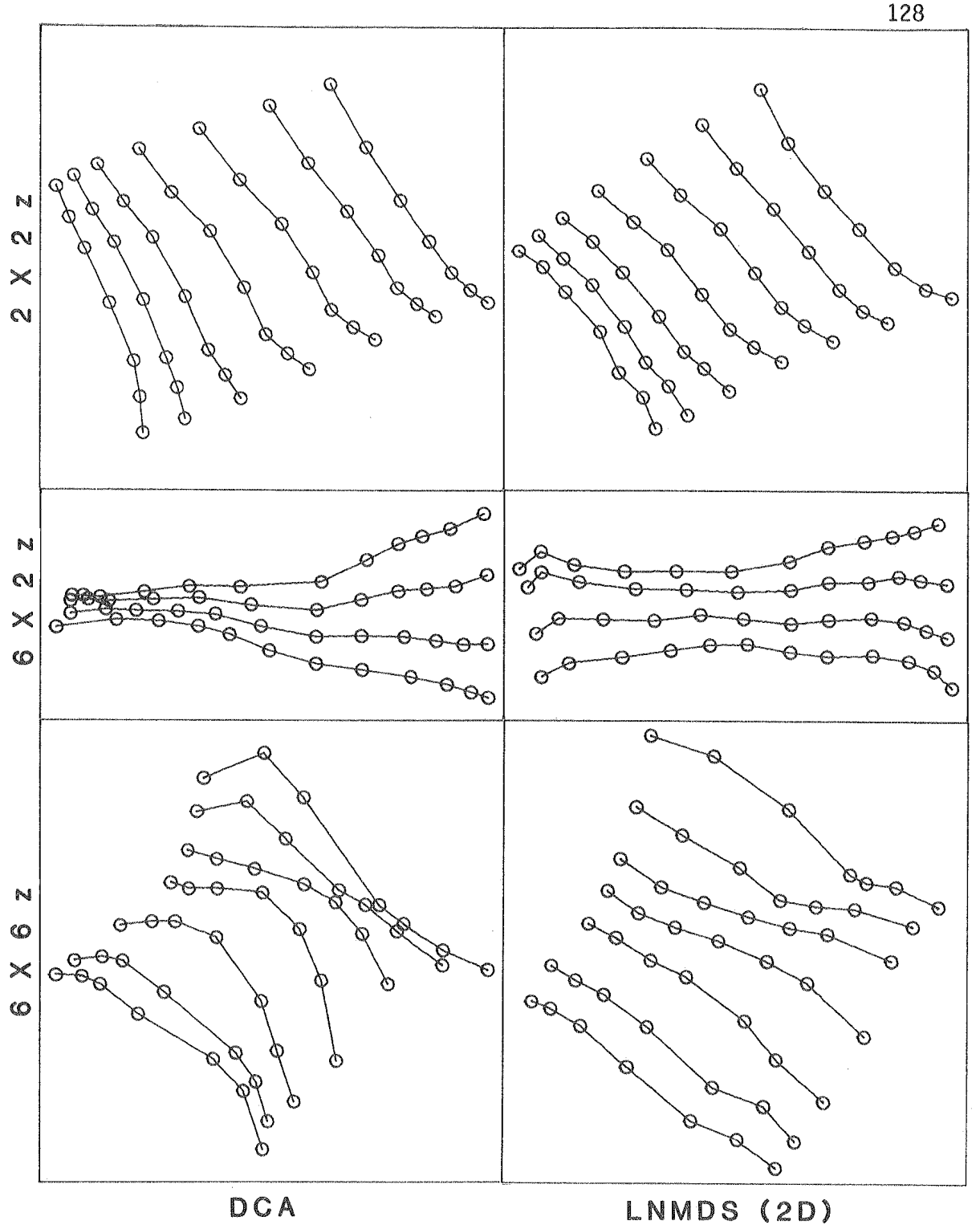


Figure 4.1 Two-dimensional ordinations of the noiseless coenoplanes in experiment 6 by DCA and LNMDS(2D). Samples joined by lines in the plots were located at identical positions along the Y axis of the model coenoplanes. Note that the LNMDS(2D) solutions are superior to those produced by DCA, especially for the 6 x 2 Z model. Each model had unimodal, symmetrical response surfaces for all species. Ordinations of these data sets by some other techniques are shown in Figures 4.2 and 4.3.

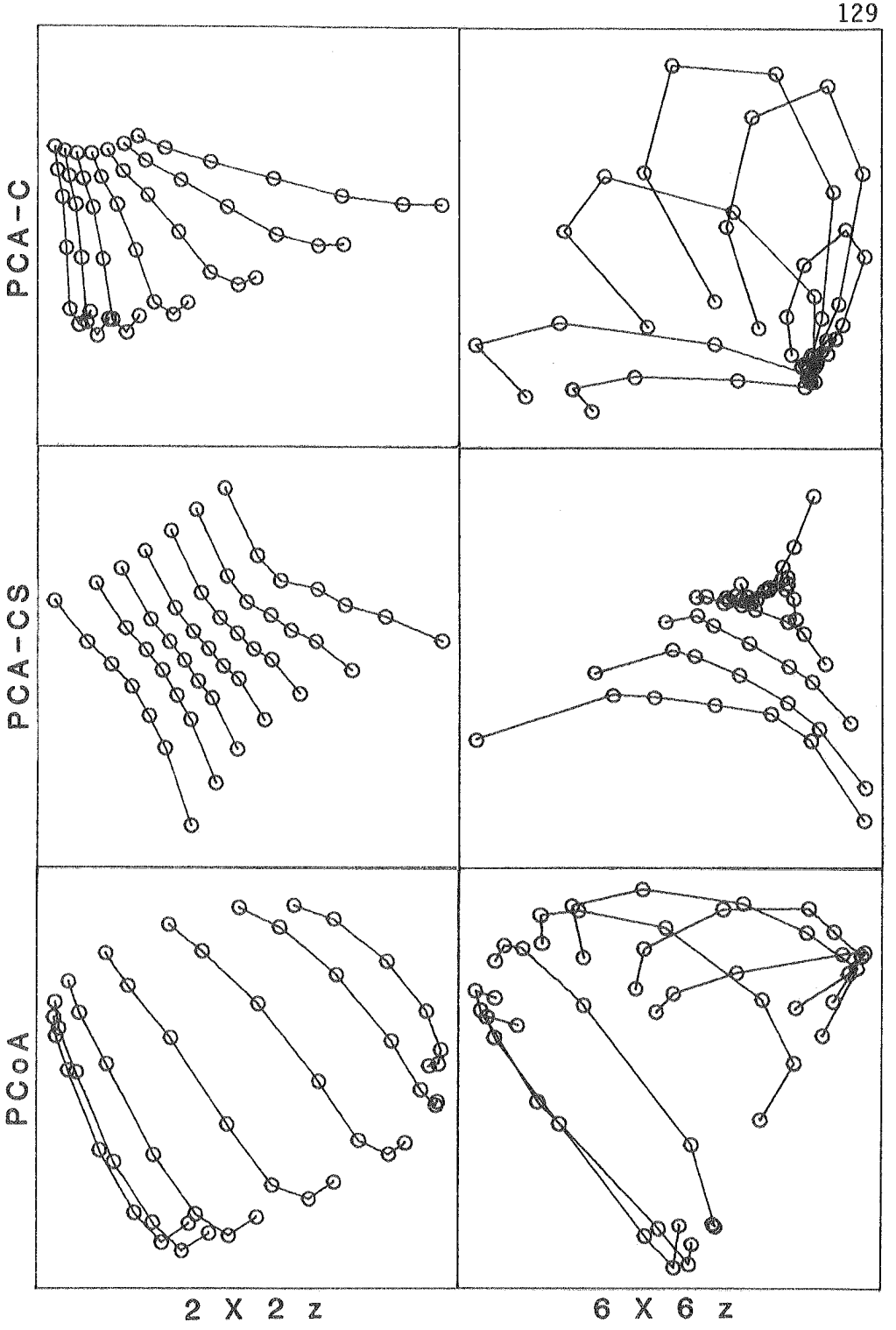


Figure 4.2 Two-dimensional sample ordinations produced by PCA-C, PCA-CS and PCoA for the noiseless 2 x 2 Z and 6 x 6 Z coenoplanes in experiment 6. Samples joined by lines in the plots were located at identical positions on the Y axis of the model coenoplanes. Note the severe curvilinear distortion of the 6 x 6 Z coenoplane by all three methods and the lesser distortion, with slight involution of coenoplane edges, of the 2 x 2 Z coenoplane by PCA-C and PCoA. Each model had unimodal, symmetrical response surfaces for all species.

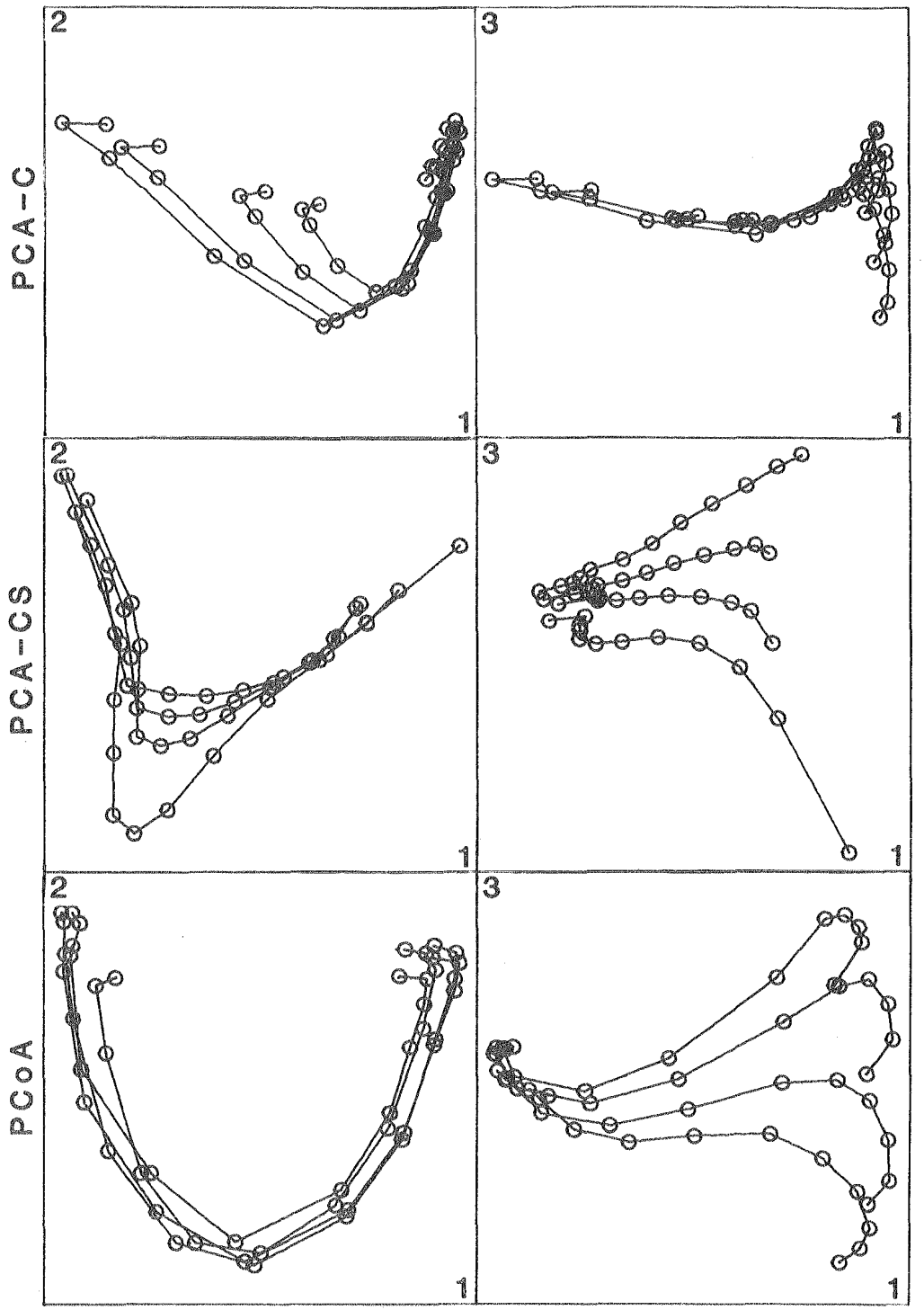


Figure 4.3 Three-dimensional ordinations produced by PCA-C, PCA-CS and PCoA for the noiseless 6 x 2 Z coenoplane in experiment 6. For each method, sample positions on both axes 1 v. 2 (left hand plots) and 1 v. 3 (right hand plots) are shown. Samples joined by lines in the plots were located at identical positions on the Y axis of the model coenoplane. Note that all three methods represented the primary (6Z) gradient as an arch on the first two axes and variation related to the secondary (2Z) gradient was only crudely displayed on the third ordination axis. Each model had unimodal, symmetrical response surfaces for all species.

the grid structure. Where necessary, scores on ordination axes have been reflected, so that the overall orientation of the sample grid for a given model is similar in the ordination plots for each method.

The ordination results in the absence of both quantitative and qualitative noise shall be described first. For the 2 X 2Z model, reasonable recovery of the square sampling grid on the first two ordination axes was achieved by DCA, PCA-CS and LNMDS(2D and 3D), although the grid was rotated with respect to the ordination axes in all cases (Figures 4.1 and 4.2). The LNMDS(2D) solution was somewhat better in terms of D2, than those for DCA, PCA-CS and LNMDS(3D). In the PCA-CS ordination, those samples which were extreme on the first axis of the coenoplane appeared relatively distant from the remainder. This is apparently a two-dimensional manifestation of the "outlier" effect noted in the experiments on coenoclines (see section 3.2.4). For PCA-C and PCoA (Figure 4.2) slight involution of the edges and/or corners of the 2 X 2Z coenoplane was apparent in the two-dimensional ordinations. The two-dimensional solution by PCA-C was particularly poor, the sample grid appearing much wider on the side corresponding to one end of the X axis of the coenoplane than on the other. In addition, one corner of the grid was involuted. The results for PCA-BC (not illustrated) were similar to those for PCoA.

For the "noiseless" 6 X 2Z model, both DCA and LNMDS(2D and 3D) achieved reasonable recovery of the two underlying gradients on the first two ordination axes (Figure 4.1). The LNMDS(2D) solution was best in terms of D2. In the DCA ordination, the direction of variation corresponding to the Y axis of the coenoplane was compressed towards one end of the primary gradient. In ordinations by PCoA and the PCA

variants, the second axis represented mainly a curvilinear distortion of the X axis of the coenoplane, while some of the variation related to the shorter coenoplane axis was generally visible on the third ordination axis (Figure 4.3). The solution for PCA-BC (not shown) was similar to that for PCoA, but with even greater involution of the ends of the longer coenoplane axis. For these methods, the fact that the compositional variation between samples is related to two underlying gradients, one being three times longer than the other in terms of beta diversity, would be very difficult to deduce from the ordination results.

Both DCA and LNMDS(2D and 3D) produced reasonable ordinations of the noiseless 6 X 6Z data set. In terms of D2, the LNMDS(2D) solution was best, and the lesser distortion of the sample grid by LNMDS(2D) compared with DCA is readily apparent in Figure 4.1. In the DCA ordination, the lines of samples occupying the same position along the Y axis of the coenoplane are consistently curved. Neither PCoA nor the PCA variants achieved a satisfactory representation of the underlying two-gradient structure on the first two ordination axes, due to complex curvature of the coenoplane into the third and higher dimensions. The solutions produced by PCoA (Figure 4.2) and PCA-BC (not shown) were the best among this group of methods. In the PCoA and PCA-BC ordinations, the coenoplane was curved into a dome in the space defined by the first three axes, with the edges and particularly the corners of the sample grid being folded inwards towards the centre of the ordination.

In general, the effect of the addition of quantitative noise for all three models was to introduce random scatter of samples about their

noiseless positions in each ordination, without systematic alteration of the overall configuration. The deterioration in D2 values with increasing noise levels was most marked for the 2 X 2Z model (Table 4.1). With low beta diversities on both coenoplane axes, the compositional variation due to noise becomes increasingly important, relative to that related to the gradients. For the 2 X 2Z model, the slight advantage of LNMDS(2D) over DCA persisted, even at a noise level of 0.2F. The performance of PCA-CS, which was comparable to that of DCA in the absence of noise, declined rapidly with increasing noise. Hence the PCA-CS ordination at 0.2F was markedly inferior to that produced by DCA (Table 4.1).

For the 6 X 2Z model, LNMDS(2D) solutions underwent severe deterioration at 0.2F, with the result that the RMS displacement error (D2) was almost twice the value achieved by DCA. Inspection of the LNMDS(2D) ordination for this data set revealed that the direction of variation corresponding to the X axis of the coenoplane was curved and that reversals of sample order on the shorter coenoplane axis were fairly frequent. In contrast, lines joining samples located at the same position along the second coenoplane axis never overlapped in the DCA ordination. Thus the effects of high levels of quantitative noise on LNMDS ordinations of 6 X 2Z coenoplanes are potentially severe. For the PCoA and PCA ordinations, the scatter introduced by noise combined with the curvilinear distortion of the longer gradient to make the recognition of the underlying structure in the ordinations even more difficult.

The effects of quantitative noise on DCA and LNMDS ordinations of the 6 X 6Z coenoplane were relatively minor, with LNMDS(2D) maintaining

its advantage over DCA even at a noise level of 0.2F (Table 4.1). In the ordinations by PCA and the three PCA variants, noise-induced scatter simply aggravated the already severe distortion of the underlying gradient structure.

Qualitative or presence-absence noise caused considerable deterioration in the performance of all methods, with the effects being most severe for the 2 X 2Z model. PCA-CS achieved the best solution for the 2 X 2Z model with qualitative noise, and the underlying two-gradient structure was still recognisable in the arrangement of the samples on the first two ordination axes, although highly distorted. Ordinations of this data set by the other methods, including DCA and LNMDS(2D), were plagued by numerous reversals of sample order on both underlying gradients. For the 6 X 2Z model with qualitative noise, none of the techniques compared was able to achieve satisfactory recovery of the underlying structure. The DCA ordination had the lowest D2 value. While it provided a reasonable representation of the variation related to the 6Z coenoplane axis on its first axis, variation related to the 2Z gradient was obscured. There was little variation between samples on the second ordination axis for about two thirds of the length of the first axis. In the case of the 6 X 6Z model, the best ordination in the presence of qualitative noise was produced by LNMDS(2D). Despite considerable noise-induced scatter, the underlying two-gradient structure was still clearly recognisable in the LNMDS(2D) ordination. The DCA ordination was next best, although its D2 value was almost twice that for LNMDS(2D) and the sample grid appeared severely deformed on the first two axes.

As might be expected, the greatest reductions in ordination efficacy were observed when both qualitative and quantitative noise were applied simultaneously. Under these circumstances, none of the methods studied was able to achieve a reasonable recovery of the underlying structure for the 2 X 2Z model. With the 6 X 2Z model, the DCA ordination was superior to that produced by LNMDS, but it was nevertheless regarded as a poor solution. In the case of the 6 X 6Z model, the advantage of LNMDS(2D) over DCA, which was noted above in the presence of qualitative noise only, was reversed when quantitative errors were introduced as well (Table 4.1).

4.2.4 Discussion and Conclusions

The results of this experiment indicate that both LNMDS and DCA are capable of reasonable recovery of the underlying structure of coenoplanes in which species response surfaces are unimodal and symmetrical. When two dimensions were specified, the ordinations produced by LNMDS were generally superior to the DCA solutions. This contrasts with the results reported in the previous chapter (section 3.2), for coenoclines with symmetrical response curves. In that case, LNMDS consistently failed to improve on the DCA ordinations. When three dimensions were allowed for LNMDS in the present experiment, the projections of the samples on the first two axes generally defined a configuration only slightly inferior to the two-dimensional solution, in terms of D2. Hence the specification of the correct underlying dimensionality for LNMDS does not appear to be as critical when there is more than one underlying gradient, as it is in the unidimensional case.

The superiority of LNMDS over DCA was most marked for noiseless

data sets derived from the 6 X 2Z and 6 X 6Z coenoplanes. However, the introduction of quantitative and/or qualitative noise sometimes tipped the balance in favour of DCA, especially for the 6 X 2Z model. Nevertheless, the results do suggest that the greater computational cost involved in LNMDS compared with DCA is repayed by a corresponding improvement in ordination efficacy. This conclusion is at variance with that of Gauch, Whittaker and Singer (1981). They found that DCA ordinations of data from Gaussian models with more than one underlying gradient were, generally, better than those produced by various forms of NMDS, including a "local" variant similar to that studied here. One possible explanation for the discrepancy is that all their ordinations by LNMDS used random initial configurations, and entrappment at local minima may have occurred. Indeed, problems with local minima were reported in ordinating data from a coenoplane of comparable beta diversity to the 6 X 2Z model used in the present study. In the current experiments, the setting of similarities between samples with no species in common to "missing" may also have improved the performance of LNMDS. Gauch, Whittaker and Singer (1981) did not employ this procedure.

The curvilinear distortion of underlying gradients in PCA and PCoA ordinations is the result of the non-linear relationship between sample resemblance and the separation of samples along the underlying gradients. This distortion gave rise to even greater problems for the interpretation of the ordinations of simulated coenoplanes than those observed previously for coenoclines (section 3.2). The vulnerability of PCA to curvilinear distortion has been well established by previous studies using Gaussian coenoplanes. Austin and Noy-Meir (1971) and Gauch, Whittaker and Wentworth (1977) noted that the degree of curvature

of coenoplanes in PCA ordinations was reduced by certain data standardisations, especially standardisation by species standard deviation or Bray-Curtis double standardisation. The present experiment confirms these observations. The general order of performance of the PCA variants (from best to worst) was PCA-CS > PCA-BC > PCA-C. The amount of curvilinear distortion in PCoA ordinations (using the percentage similarity coefficient) was generally comparable to that for PCA-BC.

The potential interpretative difficulties arising from curvilinear distortion were most marked with the 6 X 2Z and 6 X 6Z models. With the 6 X 2Z model, the curvilinear distortion of the primary (6Z) gradient prevented the effective representation of the variation related to the secondary (2Z) coenoplane axis by PCoA and all the PCA variants (Figure 4.3). Even in three dimensions, none of these techniques effectively displayed the separation of samples along the secondary gradient in all parts of the curved primary gradient. The recognition of the fact that the inter-sample variation was related to two underlying gradients (one with three times the beta diversity of the other) would be extremely difficult given these ordination results. Complex curvature of the 6 X 6Z coenoplane in the PCA and PCoA ordinations (Figure 4.2) would also hamper the correct interpretation of the underlying gradient structure. In the case of PCoA, PCA-BC and PCA-CS, a careful examination of the distributions of environmental variables in the first three or four dimensions of the ordinations might suggest the underlying two-gradient structure to a perceptive investigator. Neverthless, the goals of indirect gradient analysis are better served by methods which represent variation related to k gradients on the first k ordination axes, without curvilinear distortion. The present experiment suggests

that, if species response surfaces are symmetrical and unimodal, PCoA and PCA can only achieve this goal when the beta diversities of both underlying gradients are less than about 3Z.

4.3 Experiment 7 : The Joint Effects of Response Surface Shape and the Relative Beta Diversities of Coenoplane Axes

4.3.1 Introduction

All previous comparative evaluations of ordination methods using simulated coenoplanes have been based on the assumption that species response surfaces are of Gaussian form (Austin and Noy-Meir 1971; Gauch, Whittaker and Wentworth 1977; Fasham 1977; Gauch Whittaker and Singer 1981; Prentice 1980). The study of Austin (1976b) and the experiments with simulated coenoclines reported in Chapter 3 have indicated that the performance of some ordination methods is affected by variation in response curve shape. The present experiment examines the effects on ordinations of variation in the shape of response surfaces in simulated coenoplanes.

4.3.2 Methods

In the experiments with simulated coenoclines described in the previous chapter, the effects of response curve shape were studied only at a beta diversity of 6Z. Similarly, practical limitations restricted the present experiment to simulated coenoplanes with beta diversities of 6 X 2Z and 6 X 6Z. Within each of these categories of beta diversity, models representing six different types of response surface shape were generated. Three replicates of each type of model were prepared, using different random number seeds. Details of the six response surface types were as follows :

(1) Symmetrical - all species were given symmetrical, unimodal response surfaces, with powers α and γ set at 4.0 for both X and Y axes of the coenoplane. Modal abundances were assigned from a lograndom distribution, on the range 1 to 100. The standard deviations of the ranges of the response surfaces on both X and Y axes were set at 0.3 times the average value. In allocating the positions of species modes, no segmentation of the coenoplane was performed. Those 15% of species with the largest abundance surface integrals were designated as "major", and their modes were relocated to ensure equitable spacing. Rotation angles for the response surfaces of all species were set at zero. These models were of the same type as those used in experiment 6. The 6 X 2Z and 6 X 6Z models employed in that experiment were used as the first replicate of their respective categories in the present experiment.

(2) Slightly skewed - response surfaces for all species had powers α=4.0 and γ=2.0 on both the X and Y axes of the coenoplane. This resulted in slight skewness to the right on each axis. The allocation of the other response surface parameters followed the same procedures described for the symmetrical models.

(3) Highly skewed - all species had response surfaces highly skewed to the right on both coenoplane axes, with powers α=4.0 and γ=1.0. Other details were the same as for the symmetrical models.

(4) Mixed skewness - for all species, powers α and γ on both coenoplane axes were each randomly allocated on the range 1.0 to 4.0. This produced unimodal response surfaces of various shapes, ranging from symmetrical to highly skewed in either direction on

one or both coenoplane axes. Once again, other parameters were allocated in the same manner as they were in the symmetrical models.

(5) Competition Models with Cmax=0.2 - "physiological" response surfaces for all species were slightly skewed, with powers α=2.0 and γ=1.0 on both coenoplane axes. Modal abundances were allocated from a lograndom distribution, on the range 5 to 100. The standard deviations of species ranges on both the X and Y axes of the coenoplane were set at 0.5 times the average value. In allocating the positions of species modes, the coenoplane was not segmented. Those 20% of the species with the largest abundance surface integrals were designated "major", but the positions of the modes of major species were not readjusted. "Competition" between species was introduced in the manner described in Chapter 2, section 2.1.5.1. The upper limit for the linear interaction coefficients (Cmax) was set at 0.2, while the "protection factor" for minor species (Clim) was given a value of 0.4. These values were chosen following experience with the coenocline models, in order to produce "ecological response surfaces" displaying the shouldered and irregularly skewed forms sometimes observed in direct gradient analyses. With Cmax=0.2, the interactions between species were generally not sufficiently powerful to produce many bimodal or multimodal surfaces.

(6) Competition Models with Cmax=0.4 - these models were identical to those just described, except that the value of Cmax was set at 0.4. This resulted in interaction coefficients of twice the magnitude of those employed in the corresponding replicate with Cmax=0.2. Consequently, bimodal and multimodal "ecological

response surfaces" were more common in these models.

The resulting 36 data sets were ordinated using each technique and RMS displacement errors (D2 and D3) were computed. Ordination configurations were plotted and examined.

4.3.3 Results

The performance statistics for the 6 X 2Z models are presented in Table 4.2, while those for the 6 X 6Z models are given in Table 4.3. The results for the 6 X 2Z models will be described first.

With all of the 6 X 2Z models, the curvilinear distortion of the 6Z gradient and the consequent obscuring of variation on the 2Z gradient, marred all ordinations by PCoA and the three PCA variants, irrespective of the shape of response surfaces in the models. Hence, major interest was centred upon the relative performance of DCA and LNMDS - the techniques which performed best with the symmetrical 6 X 2Z model in experiment 6. Inspection of the performance statistics for all the models with unimodal curves (symmetrical, slightly skewed, highly skewed and mixed skewness), showed that the success of DCA relative to LNMDS varied from model to model. There was no consistent bias in favour of one method or the other (Table 4.2). Examination of the ordination plots confirmed that the differences between the configurations produced by DCA and LNMDS(2D) were generally minor. However, the solutions by LNMDS(3D) were occasionally considerably worse than the LNMDS(2D) solutions, with the rectangular sample grid appearing "arched" in the first two dimensions. With both sets of competition models, the ordinations produced by LNMDS(2D) were consistently somewhat

Ordination Method	Performance Statistic	Beta Diversity 6 x 2 Z																	
		Symmetrical (α=γ=4)			Slightly Skewed (α=4,γ=2)			Highly Skewed (α=4,γ=1)			Mixed Skewness (All Powers 1-4)			Competition Models Cmax = 0.2			Competition Models Cmax = 0.4		
		Replicate			Replicate			Replicate			Replicate			Replicate			Replicate		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
DCA	D_2	6.3	5.3	7.3	9.2	4.8	6.2	9.4	8.3	6.5	7.1	8.2	6.5	5.8	6.3	4.9	5.8	6.6	5.4
	D_3	8.4	8.8	9.7	11.6	8.2	7.6	10.7	11.3	9.7	12.3	11.5	9.6	8.7	9.2	7.2	9.2	9.2	7.9
PCA-C	D_2	20.4	20.9	18.4	25.3	18.5	16.8	17.1	25.1	14.5	26.2	19.6	18.0	12.1	15.1	20.9	16.3	15.4	21.3
	D_3	20.3	20.7	19.0	24.4	18.9	16.8	20.2	25.0	17.4	23.9	20.4	18.9	15.7	14.2	22.0	17.5	14.8	22.5
PCA-CS	D_2	18.7	17.4	20.3	19.7	19.8	19.3	16.2	19.4	17.4	17.1	20.7	19.2	18.1	15.4	16.6	18.4	15.8	13.9
	D_3	19.9	20.1	21.2	21.5	19.8	19.3	18.6	20.3	20.1	18.8	19.3	19.0	16.9	17.0	16.5	17.0	17.3	16.3
PCA-BC	D_2	21.9	21.9	21.5	19.8	21.8	21.1	16.4	19.8	20.3	19.9	21.5	21.7	19.3	16.9	16.2	19.0	17.3	15.2
	D_3	20.7	20.7	21.9	20.0	21.1	20.6	19.8	18.2	19.2	19.3	20.6	20.9	17.6	18.2	17.8	17.3	18.6	17.4
PCoA	D_2	20.4	19.3	19.8	17.7	20.0	18.7	17.1	18.8	19.9	20.6	19.9	19.0	18.2	16.7	18.9	18.2	16.8	18.4
	D_3	19.8	18.9	19.2	19.2	19.3	17.4	17.7	19.1	18.2	19.7	19.9	18.7	16.6	16.0	19.1	17.4	16.2	20.1
LNMDS (2D)	D_2	4.3	7.2	5.7	8.4	5.0	6.3	5.8	13.3	5.1	8.1	9.7	6.0	5.2	5.3	3.8	5.1	5.0	4.5
LNMDS (3D)	D_2	5.3	8.0	6.8	12.7	5.0	6.4	5.9	16.1	5.9	11.1	10.5	6.4	5.9	5.4	4.3	6.2	5.4	8.2
	D_3	7.6	10.6	10.4	14.7	8.0	7.6	9.3	15.7	8.6	16.6	12.7	8.0	7.7	7.2	7.3	9.2	7.4	11.4

Table 4.2 Ordination performance statistics for experiment 7, in which simulated coenoplanes were used to investigate the joint effects on ordination of variation in the shape of species response surfaces and the relative beta diversities of coenoplane axes. The results presented are for the models with beta diversities of 6 x 2 Z.

Ordination Method	Performance Statistic	Beta Diversity 6 x 6 Z																	
		Symmetrical (α=γ=4)			Slightly Skewed (α=4,γ=2)			Highly Skewed (α=4,γ=1)			Mixed Skewness (All Powers 1-4)			Competition Models Cmax = 0.2			Competition Models Cmax = 0.4		
		Replicate			Replicate			Replicate			Replicate			Replicate			Replicate		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
DCA	D_2	9.8	19.3	14.6	11.4	16.8	11.0	19.6	10.6	11.2	15.0	9.8	9.1	12.0	7.2	9.1	11.6	8.9	9.9
	D_3	14.5	23.4	19.5	17.4	19.1	15.5	22.0	16.1	17.4	20.3	14.7	15.9	18.1	16.5	16.7	17.3	15.9	17.4
PCA-C	D_2	33.9	31.4	32.5	20.7	26.0	30.4	31.4	31.8	28.6	25.1	30.6	35.6	22.0	18.0	19.0	21.9	18.6	19.2
	D_3	34.8	30.6	32.0	24.0	27.5	29.0	33.0	33.0	30.5	27.2	30.5	32.9	26.8	22.5	23.8	25.2	22.8	24.3
PCA-CS	D_2	21.0	16.8	26.9	26.5	22.0	20.7	23.2	26.3	25.9	18.4	18.3	24.8	11.1	11.3	12.3	11.1	11.5	14.3
	D_3	25.8	24.5	28.2	26.9	26.0	26.0	26.6	27.3	27.6	25.0	24.1	25.7	20.7	20.7	21.4	20.8	20.9	21.7
PCA-BC	D_2	20.7	19.1	23.2	23.5	18.5	28.5	26.4	17.8	19.9	23.9	16.3	19.1	11.9	11.3	13.3	12.7	12.2	12.8
	D_3	26.0	25.4	27.8	26.9	25.2	27.8	29.2	25.5	24.7	27.4	23.3	26.5	21.5	20.7	22.0	21.8	21.2	21.6
PCoA	D_2	20.1	19.0	20.9	14.4	16.4	17.2	28.6	16.2	17.0	18.3	18.5	17.9	12.2	10.6	13.0	12.2	12.0	12.9
	D_3	26.0	24.7	24.7	21.7	23.5	24.2	25.4	24.6	23.6	23.3	25.0	24.7	20.8	19.6	20.7	21.1	20.1	20.8
LNMDS (2D)	D_2	6.4	8.5	9.2	9.4	7.7	7.5	12.7	6.9	9.2	7.3	9.0	7.7	7.5	6.3	7.6	6.8	8.0	7.9
LNMDS (3D)	D_2	8.5	10.3	10.3	9.8	7.8	8.1	13.7	7.4	10.5	8.1	10.6	8.0	8.1	7.4	8.8	8.6	9.3	9.3
	D_3	16.3	17.1	17.7	13.9	11.7	12.8	19.0	14.9	17.1	17.9	16.3	13.4	14.5	12.6	14.5	16.0	14.8	15.0

Table 4.3 Ordination performance statistics for experiment 7, in which simulated coenoplanes were used to investigate the joint effects on ordination of variation in the shape of species response surfaces and the relative beta diversities of coenoplane axes. The results presented are for the models with beta diversities of 6 x 6 Z.

superior (in terms of D2) to the DCA ordinations. The effect of the different values of Cmax appeared slight. In all cases, ordinations of the Cmax=0.4 models were very similar to those of the equivalent Cmax=0.2 model.

In the case of the 6 X 6Z models, the situation regarding the relative performances of DCA and LNMDS was unequivocal. D2 values for LNMDS(2D) were consistently less than those for DCA, markedly so in several cases. When three dimensions were allowed for LNMDS, the resulting ordinations were always slightly inferior to the solutions in two dimensions. Nevertheless, they were usually better than the DCA ordinations.

Two-dimensional DCA and LNMDS(2D) ordinations of one replicate of each of the symmetrical, mixed skewness and competition (Cmax=0.4) models are illustrated in Figure 4.4. These examples were specifically chosen as representative of those models for which the superiority of LNMDS(2D) over DCA was most marked. It should be noted that the relative quality of the solutions produced by DCA was often somewhat better. Nevertheless, the occasionally poor performance of DCA is disturbing.

For the 6 X 6Z models, the PCoA and PCA ordinations were often poor, due to complex curvature of the coenoplane. However, PCA-CS occasionally produced reasonable ordinations. With one of the symmetrical models and one of the competition models, PCA-CS managed to out-perform DCA, in terms of D2 (Table 4.3). Nevertheless, the PCA-CS ordinations in these cases were poor compared with the LNMDS solutions.

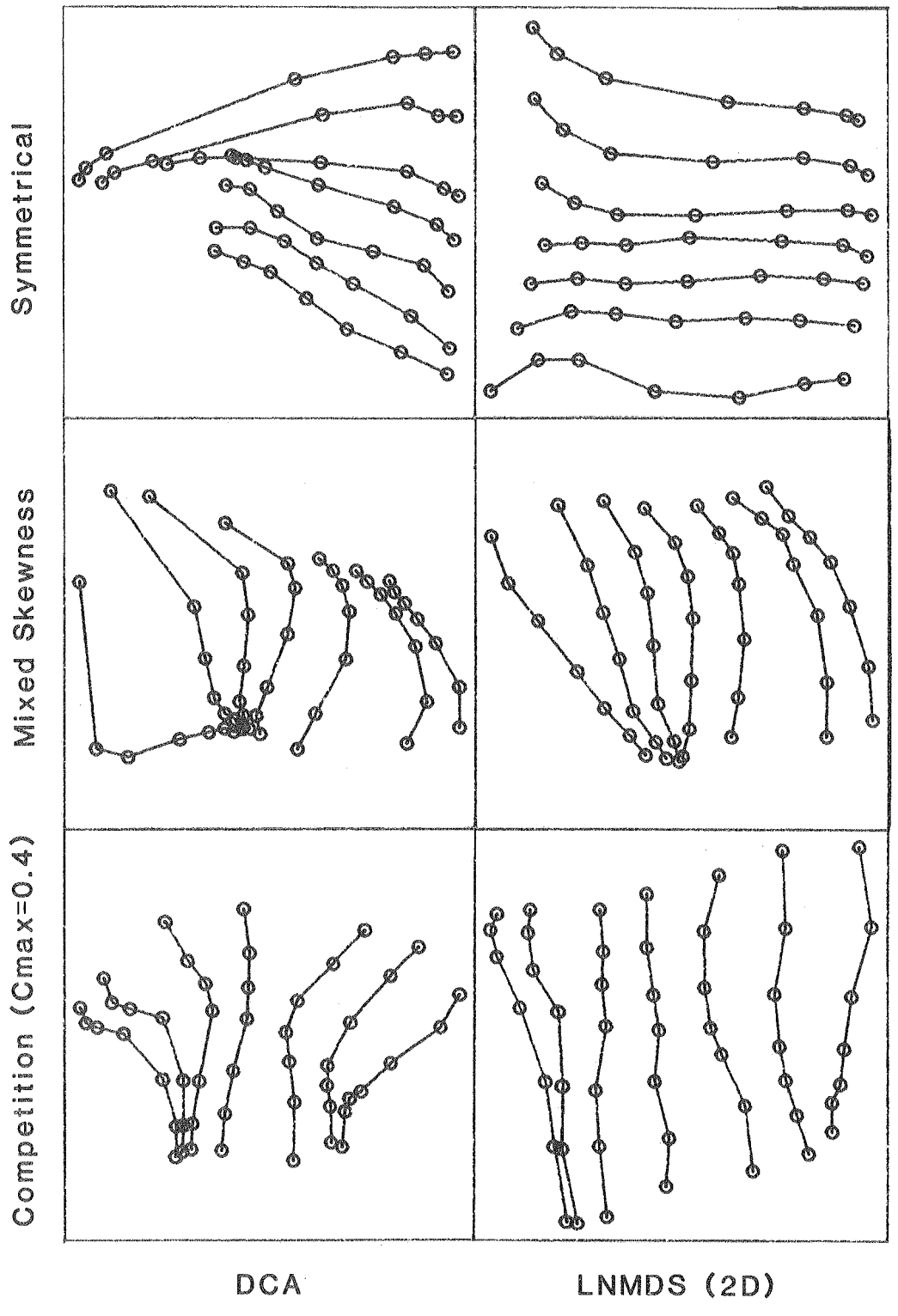


Figure 4.4 Some examples of DCA and LNMDS(2D) sample ordinations for model coenoplanes in experiment 7. The results illustrated are for one replicate model from each of the symmetrical, mixed skewness and competition (Cmax=0.4) response surface shape categories. These examples represent situations where the DCA solution was markedly inferior to the LNMDS(2D) result. In general, the divergence between the performance of the two techniques was not this great, although LNMDS(2D) always achieved better results than DCA. All models had beta diversities of about 6 x 6 Z.

4.3.4 Discussion and Conclusions

This experiment has demonstrated that both DCA and LNMDS are fairly robust to variations in response surface shape of the types studied. Neither of the techniques displayed any consistent changes in performance with response surface shape for either the 6 X 2Z or the 6 X 6Z models. With the 6 X 6Z models, LNMDS proved consistently superior to DCA. DCA ordinations for some of these models (e.g. Figure 4.4) displayed considerable distortion, the origin of which cannot be explained at present. Such severe distortion in DCA (or RA) ordinations of noiseless coenoplanes has not been previously reported, even though a number of studies have used Gaussian coenoplanes with beta diversities comparable to those used here (Gauch, Whittaker and Wentworth 1977; Fasham 1977; Prentice 1980; Gauch, Whittaker and Singer 1981). The distortion is not simply a consequence of the highly skewed or non-unimodal response surfaces used in some of the models, since it was also observed for one of the symmetrical models, and for one of those with slightly skewed response surfaces. In those cases where the DCA ordination for one of the replicates in a particular response surface shape category was considerably worse than for the other two, the relative success of LNMDS in ordinating the replicates did not parallel that of DCA. This suggests that LNMDS is not sensitive to whatever properties of the "bad" replicate had undesirable effects on DCA.

In the case of the 6 X 2Z models, where compositional variation related to the longer coenoplane axis predominated, a consistent advantage of LNMDS over DCA was not manifest. However, LNMDS performed best on all the competition models. These results are reminiscent of

those obtained in experiment 2, with simulated coenoclines (section 3.3). In that experiment, LNMDS(1D) generally out-performed DCA with the competition models, but often gave results slightly inferior to those of DCA with all the unimodal models. In combination with the present experiment, these results suggest the following tentative generalisations :

(1) When species response curves (surfaces) are unimodal, DCA generally performs better than LNMDS if there is a single underlying gradient of about 6Z. If there is a second underlying gradient, the performance of LNMDS relative to DCA improves as the beta diversity of the secondary gradient increases. The present results for the 6 X 2Z unimodal models suggest that, when the beta diversity of the shorter gradient is one third that of the longer gradient, the balance is tilted slightly in favour of LNMDS. When the beta diversities of the two gradients are approximately equal (as in the 6 X 6Z models examined here), LNMDS consistently out-performs DCA.

(2) When species response curves (surfaces) include shouldered, bimodal and multimodal forms, LNMDS generally gives superior results to DCA, irrespective of the number of underlying gradients or their relative beta diversities.

It should be noted that both these conclusions relate only to situations where the coenocline axis, or the longest coenoplane axis, has a beta diversity of about 6Z.

4.4 Experiment 8 : The Joint Effects of Response Surface Shape, the Relative Beta Diversities of Coenoplane Axes and Quantitative Noise

4.4.1 Introduction

This experiment was designed to investigate the extent to which the introduction of quantitative noise might modify the conclusions of the previous experiment. The possible effect of noise in altering the balance between DCA and LNMDS was of particular interest. The effects of qualitative noise were not studied, due to practical limitations.

4.4.2 Methods

The experiment used those 6 X 2Z and 6 X 6Z models designated as replicate one in each of the response surface shape categories in experiment 7. Ordination results in the absence of noise were thus already available. From each of these 12 "noiseless" models, two data sets were produced, using quantitative noise levels of 0.1 and 0.2F. The resulting 24 data sets were ordinated by each technique. Sample ordinations were plotted and performance statistics were computed.

4.4.3 Results

The performance statistics for the 6 X 2Z models are presented in Table 4.4 and those for the 6 X 6Z models are given in Table 4.5. For ease of comparison, the statistics for the noiseless data sets, previously given in Tables 4.2 and 4.3 respectively, are repeated here. In the PCoA and PCA ordinations, the deterioration in performance caused by quantitative noise, even at 0.2F, was generally insignificant in comparison to the severe curvilinear distortions apparent in the

Ordination Method	Performance Statistic	Beta Diversity 6 x 2 Z: Symmetrical (α=γ=4) Noise Level (F) 0.0	0.1	0.2	Slightly Skewed (α=4,γ=2) 0.0	0.1	0.2	Highly Skewed (α=4,γ=1) 0.0	0.1	0.2	Mixed Skewness (All Powers 1-4) 0.0	0.1	0.2	Competition Model Cmax = 0.2 0.0	0.1	0.2	Competition Model Cmax = 0.4 0.0	0.1	0.2
DCA	D_2	6.3	6.4	6.4	9.2	9.7	10.9	9.4	9.2	8.7	7.1	7.6	9.3	5.8	6.0	7.3	5.8	6.1	7.5
	D_3	8.4	8.4	9.3	11.6	12.1	13.5	10.7	10.9	11.3	12.3	13.2	13.7	8.7	9.0	9.7	9.0	9.2	9.4
PCA-C	D_2	20.4	20.4	20.6	25.3	26.3	25.3	17.1	18.0	18.5	26.2	26.2	26.9	12.1	12.7	14.1	16.3	15.2	15.8
	D_3	20.3	20.1	20.2	24.4	24.3	24.6	20.2	21.2	20.7	23.9	24.0	24.7	15.7	16.0	16.5	17.5	18.2	18.3
PCA-CS	D_2	18.7	18.6	20.7	19.7	18.3	20.0	16.2	15.7	19.3	17.1	16.7	18.8	18.1	17.5	18.1	18.4	18.5	18.0
	D_3	19.9	20.1	20.5	21.5	21.3	22.0	18.6	18.7	19.7	18.8	19.0	20.1	16.9	16.4	17.9	17.0	17.6	17.6
PCA-BC	D_2	21.9	22.6	21.4	19.8	20.5	19.8	16.4	18.1	20.0	19.9	21.0	17.8	19.3	19.3	19.3	19.0	19.6	19.2
	D_3	20.7	21.0	21.0	20.0	20.5	20.7	19.8	20.4	19.8	19.3	20.0	20.7	17.6	17.5	17.8	17.3	18.0	18.1
PCoA	D_2	20.4	20.4	20.3	17.7	18.2	18.5	17.1	18.2	19.8	20.6	21.5	19.3	18.2	17.7	18.1	18.2	18.7	18.5
	D_3	19.8	19.5	19.7	19.2	19.6	20.2	17.7	18.4	18.7	19.7	20.0	20.3	16.6	16.8	16.8	17.4	17.7	17.3
LNMDS (2D)	D_2	4.3	4.2	12.2	8.4	11.9	11.0	5.8	6.4	6.8	8.1	9.0	11.1	5.2	5.6	7.2	5.1	5.7	7.1
LNMDS (3D)	D_2	5.3	4.7	13.9	12.7	13.2	13.3	5.9	6.2	7.6	11.1	11.4	13.0	5.9	6.5	7.9	6.2	7.3	6.9
	D_3	7.6	9.4	12.4	14.7	15.0	15.7	9.3	10.3	10.8	16.6	16.9	17.9	7.7	8.3	10.5	9.2	7.8	9.6

Table 4.4 Ordination performance statistics for experiment 8, in which simulated coenoplanes were used to study the joint effects on ordination of variation in the shape of species response surfaces, the relative beta diversities of coenoplane axes and quantitative noise. The results presented are for the models with beta diversities of 6 x 2 Z.

Ordination Method	Performance Statistic	Beta Diversity 6 x 6 Z: Symmetrical (α=γ=4) Noise Level (F) 0.0	0.1	0.2	Slightly Skewed (α=4,γ=2) 0.0	0.1	0.2	Highly Skewed (α=4,γ=1) 0.0	0.1	0.2	Mixed Skewness (All Powers 1-4) 0.0	0.1	0.2	Competition Model Cmax = 0.2 0.0	0.1	0.2	Competition Model Cmax = 0.4 0.0	0.1	0.2
DCA	D_2	9.8	9.4	10.4	11.4	12.5	12.7	19.6	21.5	20.0	15.0	14.8	14.8	12.0	12.9	13.2	11.6	11.4	11.3
	D_3	14.5	13.2	14.7	17.4	18.4	18.3	22.0	23.0	22.2	20.3	19.0	20.1	18.1	18.1	18.3	17.3	17.2	17.6
PCA-C	D_2	33.9	33.8	33.7	20.7	23.1	20.8	31.4	31.7	32.4	25.1	25.2	25.4	22.0	23.0	24.2	21.9	21.6	21.7
	D_3	34.8	34.6	34.2	24.0	24.7	25.0	33.0	33.1	32.3	27.2	27.3	27.3	26.8	27.4	28.1	25.2	25.3	25.8
PCA-CS	D_2	21.0	20.3	18.4	26.5	22.9	27.6	23.2	22.7	19.6	18.4	23.1	24.5	11.1	8.5	10.3	11.1	9.8	10.9
	D_3	25.8	25.1	24.8	26.9	25.7	26.7	26.6	26.0	26.1	25.0	25.9	27.0	20.7	20.3	21.5	20.8	20.5	21.3
PCA-BC	D_2	20.7	22.1	23.0	23.5	21.0	20.5	26.4	21.8	32.3	23.9	27.8	21.7	11.9	12.3	13.5	12.7	13.7	15.1
	D_3	26.0	26.4	26.4	26.9	26.6	26.6	29.2	27.5	29.5	27.4	28.7	26.2	21.5	21.6	22.3	21.8	22.2	23.0
PCoA	D_2	20.1	20.6	20.7	14.4	14.6	15.1	28.6	30.3	32.6	18.3	19.0	18.4	12.2	12.2	13.1	12.2	12.8	14.3
	D_3	26.0	26.1	26.5	21.7	22.3	22.4	25.4	25.5	26.3	23.3	23.4	23.3	20.8	20.9	21.5	21.1	21.3	21.9
LNMDS (2D)	D_2	6.4	6.7	8.6	9.4	10.2	10.5	12.7	13.2	14.7	7.3	8.1	7.8	7.5	7.9	8.9	6.8	7.3	8.6
LNMDS (3D)	D_2	8.5	9.4	10.5	9.8	11.1	11.2	13.7	13.3	13.0	8.1	8.7	9.0	8.1	8.0	8.8	8.6	8.7	10.2
	D_3	16.3	17.5	18.1	13.9	15.0	16.5	19.0	18.6	18.9	17.9	18.2	18.7	14.5	15.8	17.9	16.0	16.4	18.6

Table 4.5 Ordination performance statistics for experiment 8, in which simulated coenoplanes were used to study the joint effects on ordination of variation in the shape of species response surfaces, the relative beta diversities of coenoplane axes and quantitative noise. The results presented are for the models with beta diversities of 6 x 6 Z.

ordinations of the noiseless models. In no case did the introduction of noise cause the performance of DCA or LNMDS to deteriorate to a level approaching that of PCoA or the PCA variants. Hence the following discussion will be concerned mainly with the relative performance of DCA and LNMDS.

In the case of the 6 X 2Z models, both DCA and LNMDS proved reasonably robust to the introduction of quantitative noise (Table 4.4). With a few exceptions, the relative success of the methods with the noiseless models was maintained in the presence of noise. The exceptions occurred with the symmetrical and slightly skewed models. The LNMDS ordinations of the symmetrical model were better than those produced by DCA in the absence of noise (Figure 4.1) and at a noise level of 0.1F. However, at a noise level of 0.2F, the LNMDS solution was much worse than the DCA result. For the slightly skewed model, the LNMDS(2D) ordination was slightly superior to the DCA ordination in the absence of noise, but DCA gained a marginal advantage over LNMDS(2D) at noise levels of 0.1 and 0.2F.

With the 6 X 6Z models, DCA and LNMDS again displayed considerable robustness to the effects of quantitative noise, with DCA appearing somewhat less affected than LNMDS. Nevertheless, the consistent advantage of LNMDS over DCA, noted in the absence of noise in experiment 7, was always maintained, even at a noise level of 0.2F (Table 4.5).

4.4.4 Discussion and Conclusions

The results of the present experiment indicate that the overall conclusions of experiment 7 (section 4.3.4), regarding the relative performance of DCA and LNMDS, are still broadly correct in the presence of quantitative noise. The only major exception concerns the balance between DCA and LNMDS with 6 X 2Z coenoplanes. High levels of quantitative noise may affect LNMDS more severely than DCA under these circumstances, thus reducing or even reversing the advantage of LNMDS over DCA. Inspection of those LNMDS ordinations for which quantitative noise caused the greatest increases in D2 values, revealed that noise-induced scatter was greatest in the direction representing the 2Z coenoplane axis. This once again illustrates the principle that the recovery of gradients of low beta diversity is most affected by noise.

4.5 Experiment 9 : The Effects of Sample Distributions on 6 X 6Z Coenoplanes

4.5.1 Introduction

In the experiments with simulated coenoplanes reported thus far, samples have always been arranged on a regular grid. Such even sampling patterns enable systematic distortions to be readily appreciated on inspection of the sample ordinations. However, field sampling of vegetation when there are two underlying gradients is most unlikely to produce such a regular arrangement. Previous comments relating to simulated coenoclines (section 3.5.1), are readily generalised to coenoplanes. The occurrence in a landscape of sites representing various combinations of the underlying complex-gradients will usually be uneven. Hence equitable sampling of the landscape on an areal basis

will result in a greater concentration of samples in some parts of the coenoplane.

Futhermore, some combinations of the factor-complexes may not be represented in the landscape. For example, a complex-gradient related to nutrient supply may only be expressed at low altitudes. It would then be impossible to obtain any high-altitude samples representing the extremes of the nutrient gradient. Under such circumstances, the coenoplane would be T-shaped, rather than rectangular or square. In other situations, one complex-gradient may only be expressed towards the centre of another gradient. The coenoplane would then be cross-shaped. The behaviour of ordination methods in the presence of T-shaped or cross-shaped compositional patterns does not appear to have been investigated. Such situations were simulated in the present experiment by sampling square coenoplanes with T-shaped or cross-shaped patterns.

4.5.2 Methods

This experiment employed three 6 X 6Z simulated coenoplanes. They were the same models designated as replicate one in the symmetrical, highly skewed and competition model (Cmax=0.4) categories in experiment 7. Ordination results for an even sampling pattern, with samples arranged on a regular 7 X 7 grid, were thus already available. Five additional sampling arrangements were devised as follows :

(1) Random - 50 samples were distributed at random over the square coenoplane.

(2) Centre Favoured - The coenoplane was divided into 25 cells of equal area, by splitting each axis into five equal segments. Within each cell, samples were placed at random, the numbers in

each cell being selected in such a manner that the central cell and its neighbours received considerably more samples than the marginal cells. The total number of samples used was 50.

(3) Edges Favoured - The coenoplane was again divided into 25 cells in the manner just described. Samples were placed at random within each cell. The number of samples in each of the marginal cells was considerably greater than the number allocated to the central cells. The total number of samples was 49.

(4) T-shaped Pattern - This arrangement was intended to simulate the situation mentioned in the introduction, where one gradient is only expressed towards one extreme of another gradient. As before, the coenoplane was divided into 25 cells, but samples were placed in only nine of the cells, forming a T-shaped arrangement (Figure 4.5). Six samples were placed at random within each of these nine cells, giving a total of 54.

(5) Cross-Shaped Pattern - This arrangement was intended to simulate a situation where one gradient is expressed only near the centre of another gradient. Once again, the coenoplane was divided into 25 equal cells. Samples were placed in only nine of these, forming a cross-shaped arrangement (Figure 4.5). Six samples were placed at random within each of these nine cells, giving a total of 54.

The positions of samples in each of the arrangements is illustrated in Figure 4.6. The simulated coenoplanes were sampled using each of the five arrangements and the resulting 15 data sets were subjected to ordination by each technique. Performance statistics were computed and plots of the sample ordinations were prepared and inspected.

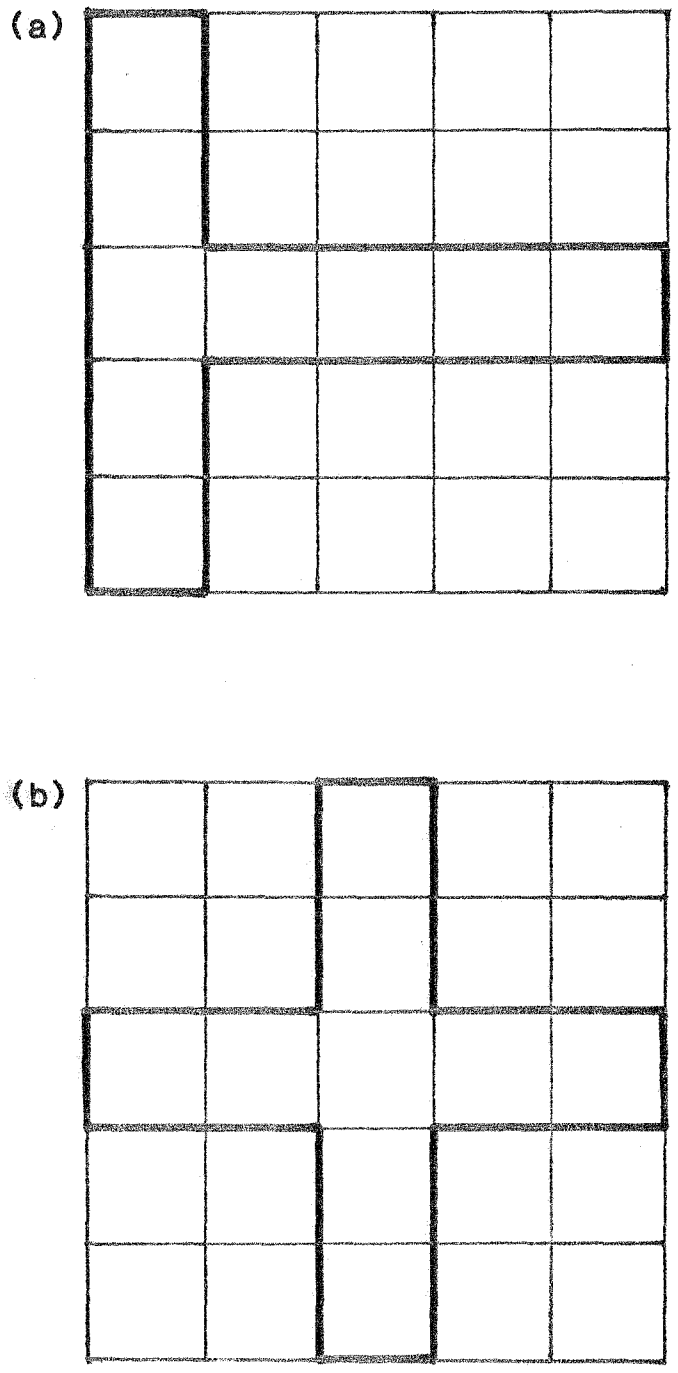


Figure 4.5 Regions of the model coenoplanes sampled to produce (a) the T-shaped and (b) the cross-shaped sampling patterns in experiment 9. In both cases six samples were placed at random within each of the nine cells enclosed by the bold lines.

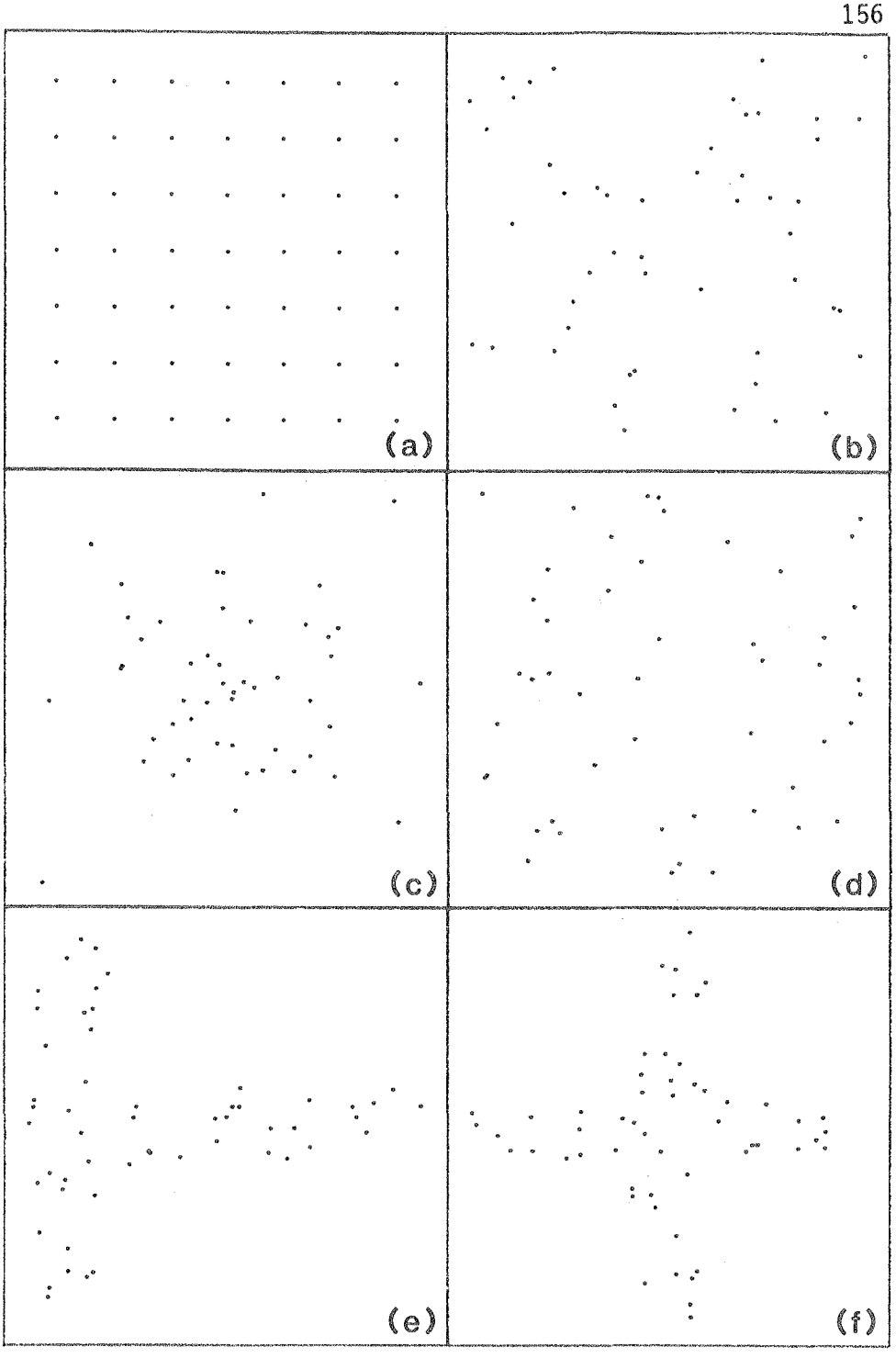


Figure 4.6 Locations of samples in the six sampling patterns employed in experiment 9. The axes of the plots represent the X and Y axes of the model coenoplanes, and each point indicates a sample. The arrangements are: (a) even, (b) totally random, (c) favouring the central region, (d) favouring the edges, (e) T-shaped and (f) cross-shaped.

4.5.3 Results

The performance statistics are presented in Table 4.6, where the results for even sampling are also given for comparison. Sample ordinations by DCA and LNMDS(2D) (axis 1 v. 2) for the symmetrical and highly skewed models with the cross-shaped sampling pattern are given in Figure 4.7. In Figure 4.8, sample ordinations by DCA (axes 1 v. 2 and 1 v. 3), LNMDS(2D) and PCA-CS (axes 1 v. 2) are presented for the competition model with the cross-shaped sampling arrangement. Figure 4.9 illustrates the ordination configurations (axes 1 v. 2) produced by DCA and LNMDS(2D) for the symmetrical, highly skewed and competition models using the T-shaped sampling pattern. In all these ordination plots, the approximate direction of variation corresponding to the X axis of the coenoplane is indicated by a solid curve and that corresponding to the Y axis is represented by a dotted line.

For the symmetrical models, the superiority of LNMDS(2D) over DCA, which was noted with even sample placement, persisted with all other sampling patterns examined, except the cross-shaped arrangement. In the latter case, the DCA ordination had a lower D2 value than the corresponding LNMDS(2D) solution and inspection of the ordinations showed that the "arms" of the cross were subjected to greater curvature in the LNMDS(2D) ordination (Figure 4.7). Variation in ordination efficacy between sampling patterns, as expressed by D2, was considerably greater for DCA than for LNMDS(2D). The worst performance by DCA occurred with random sample placement, where the D2 value was more than three times the value for LNMDS(2D).

Ordination Method	Performance Statistic	Symmetrical ($\alpha=\gamma=4$) Sample Arrangement						Highly Skewed ($\alpha=4$, $\gamma=1$) Sample Arrangement						Competition Model with Cmax=0.4 Sample Arrangement					
		Even	Random	Centre	Edges	T	+	Even	Random	Centre	Edges	T	+	Even	Random	Centre	Edges	T	+
DCA	D_2	9.8	21.8	8.8	12.7	17.2	5.9	19.6	26.8	17.6	15.2	17.5	13.0	11.6	18.4	9.3	11.6	10.4	22.9
	D_3	14.5	24.5	11.2	17.9	19.4	8.1	22.0	28.1	19.0	20.8	17.8	13.5	17.3	21.4	13.6	17.7	12.2	20.7
PCA-C	D_2	33.9	36.1	25.8	34.8	29.6	25.2	31.4	33.6	24.8	31.3	15.8	21.4	21.9	22.9	20.4	22.7	12.9	24.6
	D_3	34.8	36.8	25.7	35.6	29.4	24.5	33.0	29.8	25.3	33.3	18.4	20.9	25.2	26.7	22.1	26.2	18.0	20.2
PCA-CS	D_2	21.0	21.3	21.7	20.6	20.0	12.9	23.2	22.2	25.3	23.9	14.3	19.9	11.1	15.0	21.6	15.4	8.6	12.0
	D_3	25.8	26.9	21.1	26.8	22.3	17.1	26.6	26.9	21.2	29.2	20.9	19.7	20.8	22.9	18.8	23.4	18.8	17.0
PCA-BC	D_2	20.7	22.6	17.9	23.2	18.9	14.9	26.4	27.9	23.7	23.6	21.3	25.5	12.7	13.4	16.2	14.0	10.8	11.7
	D_3	26.0	27.5	20.8	27.4	21.9	17.9	29.2	30.8	23.9	29.6	24.3	22.9	21.8	23.3	19.9	23.4	19.1	18.0
PCoA	D_2	20.1	28.1	20.7	18.6	17.6	16.1	28.6	22.3	22.0	29.9	14.2	25.7	12.2	14.5	17.2	12.9	10.3	16.5
	D_3	26.0	26.4	21.7	27.8	21.3	19.0	25.4	25.2	22.2	26.5	19.2	19.8	21.1	22.8	20.3	23.3	18.8	18.3
LNMDS (2D)	D_2	6.4	6.7	7.0	8.0	9.0	8.3	12.7	14.1	12.1	14.7	12.0	11.9	6.8	7.0	6.8	7.5	8.8	22.9
LNMDS (3D)	D_2	8.5	7.8	9.4	8.7	9.4	9.5	13.7	15.6	14.1	15.0	12.9	11.9	8.6	9.2	7.5	10.5	9.5	16.9
	D_3	16.3	18.9	13.3	14.8	12.8	12.3	19.0	19.7	16.4	22.3	15.0	14.7	16.0	16.7	13.9	19.2	14.2	18.2

Table 4.6 Ordination performance statistics for experiment 9, in which simulated coenoplanes were used to investigate the joint effects on ordination of variation in the shape of species response surfaces and the arrangement of samples. All models had beta diversities of 6 x 6 z and no noise was added.

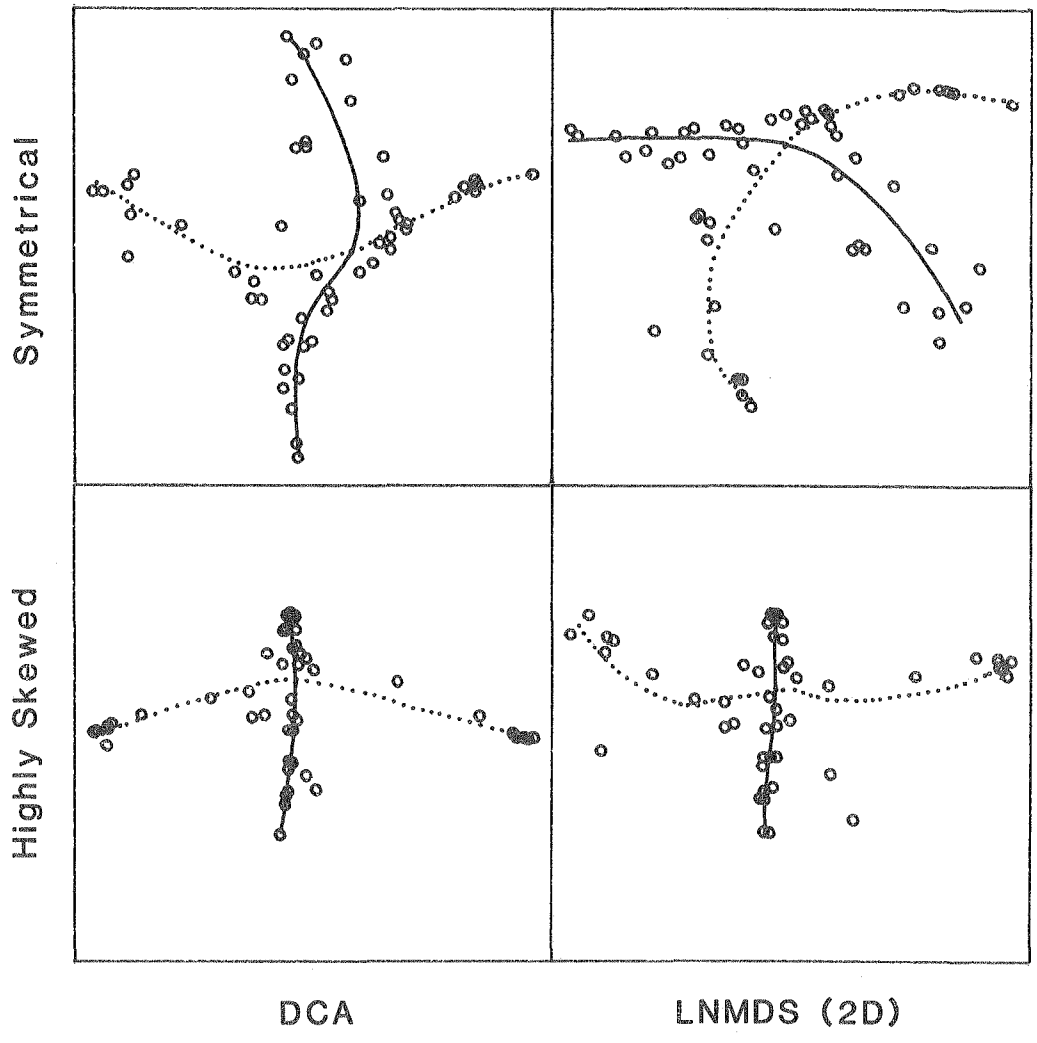


Figure 4.7 Two-dimensional ordinations produced by DCA (left) and LNMDS(2D) (right) for the symmetrical and highly-skewed model coenoplanes in experiment 9, using the cross-shaped sampling pattern. The open circles represent samples. The approximate direction of the X axis of the coenoplane is indicated by a solid line and that corresponding to the Y axis is shown as a dotted line. Each coenoplane had a beta diversity of about 6 x 6 Z and no noise was added.

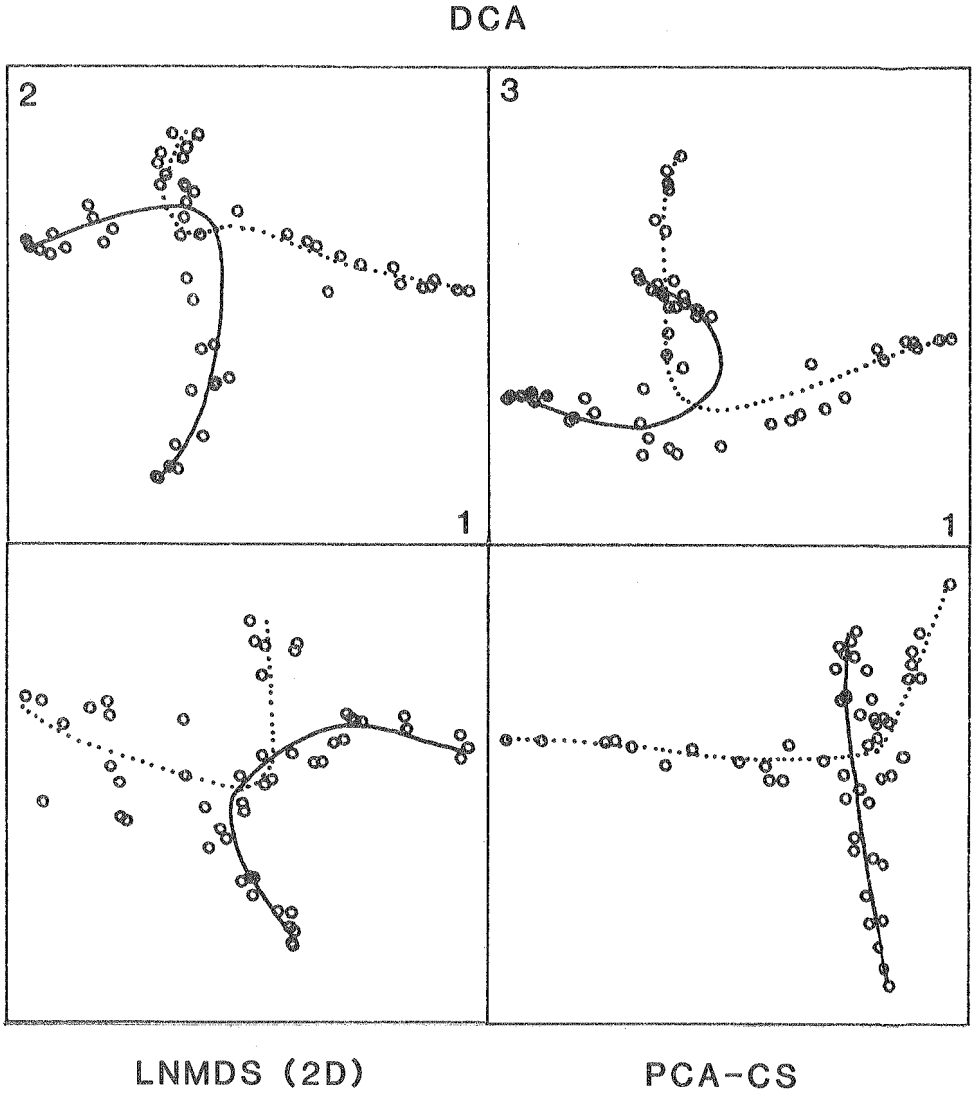


Figure 4.8 Ordinations of the competition model in experiment 9, using the cross-shaped sampling pattern. The upper two plots are axes 1 v. 2 and 1 v. 3 of the DCA solution. The two-dimensional ordinations by LNMDS(2D) and PCA-CS are shown at the lower left and right respectively. Samples are represented by open circles. The solid curves indicate the approximate direction of the X axis of the model coenoplane, while the direction corresponding to the Y axis is shown as a dotted line. The coenoplane had a beta diversity of about 6 x 6 Z and no noise was added.

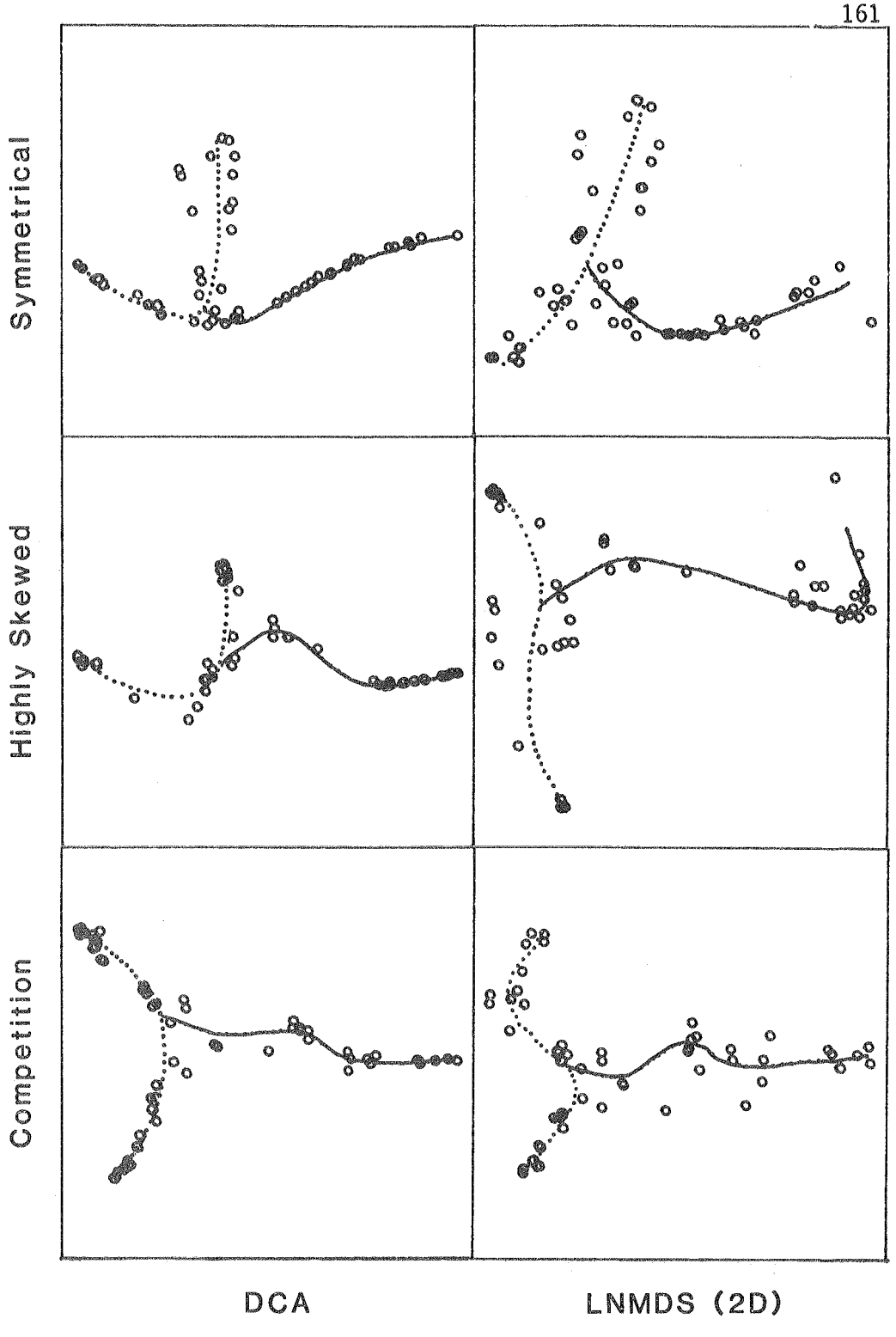


Figure 4.9 Two-dimensional ordinations by DCA (left) and LNMDS(2D) (right) of data derived from the symmetrical, highly skewed and competition models in experiment 9, using the T-shaped sampling pattern. Each coenoplane had a beta diversity of about 6 x 6 Z and no noise was added. Samples are represented as open circles, and the approximate directions of the X and Y axes of the coenoplane are indicated by the solid and dotted lines respectively.

Results for the models with highly skewed response surfaces were similar. However, LNMDS(2D and 3D) out-performed DCA with all sampling patterns, including the cross-shaped pattern. Once again the D2 values for DCA displayed notably greater variation between sampling arrangements than those for LNMDS(2D), and DCA performed worst with the random sampling pattern. With the T-shaped sampling pattern PCoA, PCA-CS and PCA-BC all out-performed DCA but not LNMDS(2D). However, inspection of the ordinations revealed that only the PCA-CS solution should be regarded as superior to that produced by DCA. Involution of extreme samples on one or both of the underlying gradients was apparent in the PCoA and PCA-BC ordinations. Curvilinear distortion of the Y axis of the coenoplane appeared to be the major reason for the poor performance of DCA with the T-shaped sampling pattern (Figure 4.9). Even the LNMDS(2D) ordination, which had the lowest D2 value, displayed an undesirable bunching of samples at both ends of the Y gradient and slight involution of extreme stands on the X gradient (Figure 4.9). Thus PCA-CS may be regarded as the most successful technique with this highly skewed model and the T-shaped sampling pattern. With the cross-shaped pattern, LNMDS(2D) produced the best ordination, although the DCA ordination was only slightly inferior (Figure 4.7). Both ordinations greatly exaggerated the length of the Y axis of the coenoplane, relative to that of the X axis. Consequently, neither could be regarded as a truly satisfactory representation of the underlying structure.

The most accurate ordinations of the competition model with the random sampling pattern, the arrangement favouring the centre of the coenoplane and the arrangement favouring the edges were produced by

LNMDS(2D). DCA achieved the next best results for the sampling patterns favouring the centre and edges of the coenoplane. However, as observed with both the symmetrical and highly skewed models, random sampling led to a particularly poor DCA solution. Hence with random sampling, PCA-BC, PCoA and PCA-CS were able to out-perform DCA (Table 4.6). The most accurate recovery of sample positions for the T-shaped sample pattern was achieved by PCA-CS. The D2 value for the LNMDS(2D) solution was only marginally greater. Although D2 values for DCA, PCA-BC and PCoA ordinations were nearly equal, both the PCA-BC and PCoA ordinations were marred by slight involution of gradient extremes. In the case of the cross-shaped sampling arrangement, both DCA and LNMDS(2D) ordinations were considered unsatisfactory. The DCA sample ordination on the first three axes is illustrated in Figure 4.8. Both underlying gradients have been bent approximately at right angles near the point corresponding to the centre of the coenoplane. Consequently, ordination axes 1 and 2 each display about half the variation along the X gradient and half that along the Y gradient. Samples representing one half of the Y gradient are bunched together towards the upper end of the second axis, although they are separated on the third axis. A similar type of distortion occurred with LNMDS(2D). The best ordination of the competition model with the cross-shaped sampling pattern was that produced by PCA-CS (Figure 4.8). For this method, the only systematic distortion in two dimensions was a bending of one end of the Y gradient. The PCA-BC solution was marred by curvilinear distortion and slight involution of one end of each gradient, despite its slightly lower D2 value (Table 4.6).

4.5.4 Discussion and Conclusions

This experiment has shown that the performance of ordination techniques can be profoundly influenced by the manner in which samples are distributed over a coenoplane. Hence the relative success of techniques with data derived by regular sampling is not always indicative of their performance with other sampling patterns. Of all the methods tested, LNMDS(2D) appeared least sensitive to variations in the sampling pattern. For a given model, the D2 values for LNMDS(2D) were remarkably consistent between sampling arrangements, the only exception being a marked deterioration in performance for the competition model with the cross-shaped pattern (Table 4.6). This may have been due to the combination of the poor starting configuration provided by DCA and entrappment at a local minimum.

In contrast, DCA showed considerable variation in performance with sampling patterns, giving particularly poor results with random sampling. It may be tentatively suggested that better ordinations are produced by DCA when samples cover the range of compositional variation fairly evenly. The prediction of Mohler (1981), that sampling favouring the edges of coenoplanes will increase the efficacy of DCA ordinations is not supported by the present results. The D2 values when sampling favoured the edges of the coenoplanes were not consistently lower than the corresponding values for regular sampling or sampling favouring the central region. It is therefore recommended that field ecologists should endeavour to sample the full range of environmental and compositional variation as evenly as possible, rather than concentrating sampling effort on sites thought to represent the extremes of

environmental gradients, as suggested by Mohler (1981).

For all three models, the ordination results with the T-shaped and cross-shaped sampling patterns were generally unsatisfactory. Those ordinations considered best were often marred by curvilinear distortion of one or both gradients. Consequently, a given ordination axis often confounded variation on both underlying gradients.

With the T-shaped sampling pattern, DCA tended to reorient one half of the Y gradient (which corresponds with the cross-bar of the T) so that it was more or less co-linear with the X gradient. This gives the appearance of a single, longer compositional gradient with a short side branch (Figure 4.9). LNMDS(2D) was generally more successful, in that the two gradients appeared fairly straight and approximately at right angles to each other in the ordinations. Interpretation of DCA ordinations should take into account the possibility of this type of distortion.

In the case of the cross-shaped sampling pattern, DCA achieved a good reconstruction of the underlying gradients for the symmetrical model. However, a slight arching of both gradients in the ordination suggests that the detrending process was not fully effective. The corresponding LNMDS(2D) ordination was somewhat inferior, since arching of both gradients was more pronounced (Figure 4.7). Both DCA and LNMDS(2D) recovered the underlying gradients in the highly skewed model as both straight and perpendicular. Both methods exaggerated the length of the Y gradient relative to the X gradient and also the amount of lateral variation (in the direction of the X gradient) which occurred on the two "arms" of the Y gradient. The poor solutions produced by both

DCA and LNMDS(2D) with the competition model and the cross-shaped sampling arrangement have already been described. In this particular model, the strength of compositional affinities between samples located on different "arms" of the cross was apparently insufficient to ensure that the correct orientation of the "arms" relative to each other was maintained in the ordinations.

The present study is apparently the first to study the effects on ordinations of T-shaped and cross-shaped sampling patterns. As discussed in the introduction (section 4.5.1), these arrangements were intended to simulate field situations in which a particular environmental gradient is only fully expressed within a limited range of another gradient. Although these results are at best preliminary, they do suggest that even those ordination techniques considered on the basis of experiments 6 to 8 to be among the best currently available (i.e. LNMDS and DCA), may sometimes give unsatisfactory solutions in these situations. LNMDS appears to be somewhat more reliable than DCA under these circumstances. Further work on this problem is necessary.

In summary, the results of the current experiment suggest that the general advantage of LNMDS over DCA with evenly sampled coenoplanes is maintained with alternative sampling patterns.

4.6 General Conclusions

The current experiments with simulated coenoplanes suggest that, of the methods examined, LNMDS generally recovers the underlying gradient structure most accurately. DCA was the next most successful technique, but it produced poor solutions for some models. PCoA, PCA-BC and PCA-C can only achieve satisfactory results when the beta diversity of both gradients is low (less than 3Z), although PCA-CS occasionally produces reasonable results for 6 X 2Z and 6 X 6Z models.

CHAPTER 5 : CONCLUSION

The major aim of the present study was to identify those ordination techniques which are most robust to plausible variations in vegetation-gradient models (particularly the form of response curves). Of the methods tested, the most successful in this respect was LNMDS. In this study the method was applied to a matrix of percentage similarity coefficients, with zero (i.e. indeterminate) similarities marked as "missing". DCA ordinations were used as starting configurations. With a single underlying gradient, along which all species had unimodal response curves, LNMDS could not improve upon the DCA solutions. However, for coenoclines which included some species with shouldered, bimodal or multimodal response curves, LNMDS recovered the rank order and spacing of the samples better than the original DCA ordination. When there were two underlying gradients, the results were unequivocal: LNMDS consistently improved upon the DCA result, even for coenoplanes with symmetrical, unimodal response surfaces. LNMDS also appeared to be less sensitive to variation in sampling patterns than DCA, and was more successful with T-shaped and cross-shaped compositional patterns. The major situation in which DCA sometimes recovered the structure of coenoplanes more accurately than LNMDS was for noisy, 2 X 2Z and 6 X 2Z models.

Gaussian Ordination appears to be of limited use for indirect gradient analysis. The method is only appropriate when there is one underlying gradient. It could only improve significantly on the DCA solutions, used as initial configurations, when the following conditions prevailed simultaneously: (1) response curves were unimodal and

symmetrical (or only slightly skewed), (2) quantitative noise levels were low and (3) beta diversity was less than about 6Z. The highly specific model of Gaussian Ordination makes the method undesirably sensitive to response curves which depart from the Gaussian form.

The linear ordination methods examined in the present study (i.e. PCA, PCoA) were only effective, for the purpose of indirect gradient analysis, when the beta diversities of all underlying gradients were less than about 4Z. At higher levels of beta diversity, the curvilinear distortion of underlying gradients made the interpretation of linear ordinations difficult. This was especially so for coenoplanes. The problems of curvilinear distortion were not confined to models with symmetrical, unimodal response curves, but occurred with all of the curve shapes studied.

The present results therefore suggest a preference for LNMDS (in the particular form examined) as a "general purpose" approach to indirect gradient analysis. This conclusion is at variance with that of Gauch, Whittaker and Singer (1981), who regarded DCA as generally superior to various forms of NMDS. However, they did not apply NMDS in the form used in the present study. The use of DCA solutions, rather than random starting configurations, and the setting of zero similarities to "missing" may have tipped the balance in favour of LNMDS in this study. The variation in the performance of DCA between replicate coenoplanes with the same underlying properties (see Figures 4.1 and 4.4), indicates the danger of basing conclusions about the relative merits of techniques on their performance with a limited set of models.

LNMDS gave best results when the correct dimensionality was specified. This was particularly important for coenocline models, where two-dimensional LNMDS ordinations were sometimes marred by involution. However, in the case of coenoplanes, the first two axes of the three-dimensional LNMDS solutions generally recovered the underlying structure only slightly less effectively than the two-dimensional solutions. In most cases, the three-dimensional LNMDS ordination was still a marked improvement upon the original DCA ordination. Hence the choice of the correct underlying dimensionality may not be so critical when there is more than one gradient.

The major limitation of LNMDS is that the computational cost rises non-linearly with the number of samples. Most currently available programs can only handle between 60 and 100 samples. For large numbers of samples, DCA would therefore be the method of choice for indirect gradient analysis. Alternatively, large data sets could be classified, and the cluster centroids subjected to ordination by LNMDS. However, it would be important to ensure that the classification did not submerge variation related to interesting, but relatively minor gradients. This approach was explored in Chapter 9 of this thesis.

The flexible approach to the simulation of vegetation-gradient relationships, which was employed in the current study, should prove useful in future comparative evaluations of ordination methods. As new techniques for non-linear ordination are developed (e.g. Goodall and Johnson 1982), it will be important to assess their performance with a range of models, encompassing the full range of current concepts concerning vegetation-gradient relationships. This is of particular importance for methods based on highly specific non-linear models (e.g.

Gaussian Ordination). The excellent performance of such methods on simulated data based on their underlying models is of little practical relevance, unless it can be established that such models are widely applicable to field situations.

Understanding of the nature of vegetation-gradient relationships is limited at present. Hence the development of highly specific non-linear ordination methods is probably premature. Until a well developed theory of vegetational response to gradients emerges, methods which are robust to moderate variation in the underlying model (e.g. LNMDS) would appear to be the most reliable approaches to indirect gradient analysis.

PART 2

An Integrated Ordination - Classification Analysis of the Alpine and Subalpine Plant Communitites of the Mt. Field Plateau, Tasmania.

CHAPTER 6 : INTRODUCTION

6.1 Objectives of the Study

The present study arose out of a general interest in the largely undescribed montane vegetation of Tasmania, with its highly endemic flora (Kirkpatrick and Brown 1983), and a desire to obtain field evidence bearing on some theoretical and methodological problems. The Mt. Field Plateau was chosen as a study area because of its proximity, accessibility, a relative lack of disturbance by the activities of European man and prior familiarity with the flora. The major objectives of the study may be summarised as follows:

(1) To identify and describe the major patterns of variation in the subalpine and alpine vegetation of the Mt. Field Plateau and relate these patterns to underlying environmental, or other (e.g. successional) gradients.

(2) To obtain observational evidence concerning the nature of relationships between vegetation and environmental gradients. Such evidence is of fundamental importance to theoretical plant ecology and is also required as a basis for the development of the most appropriate procedures for indirect gradient analysis (see Part 1 of this thesis).

(3) To examine some methodological problems in both direct and indirect gradient analysis. These include (a) the use of more rigorous methods for fitting response curves in direct gradient analysis, (b) the comparative evaluation of the ordination methods studied in Part 1 using real data, (c) the effects of data type and sample size on ordination results and (d) the potential value

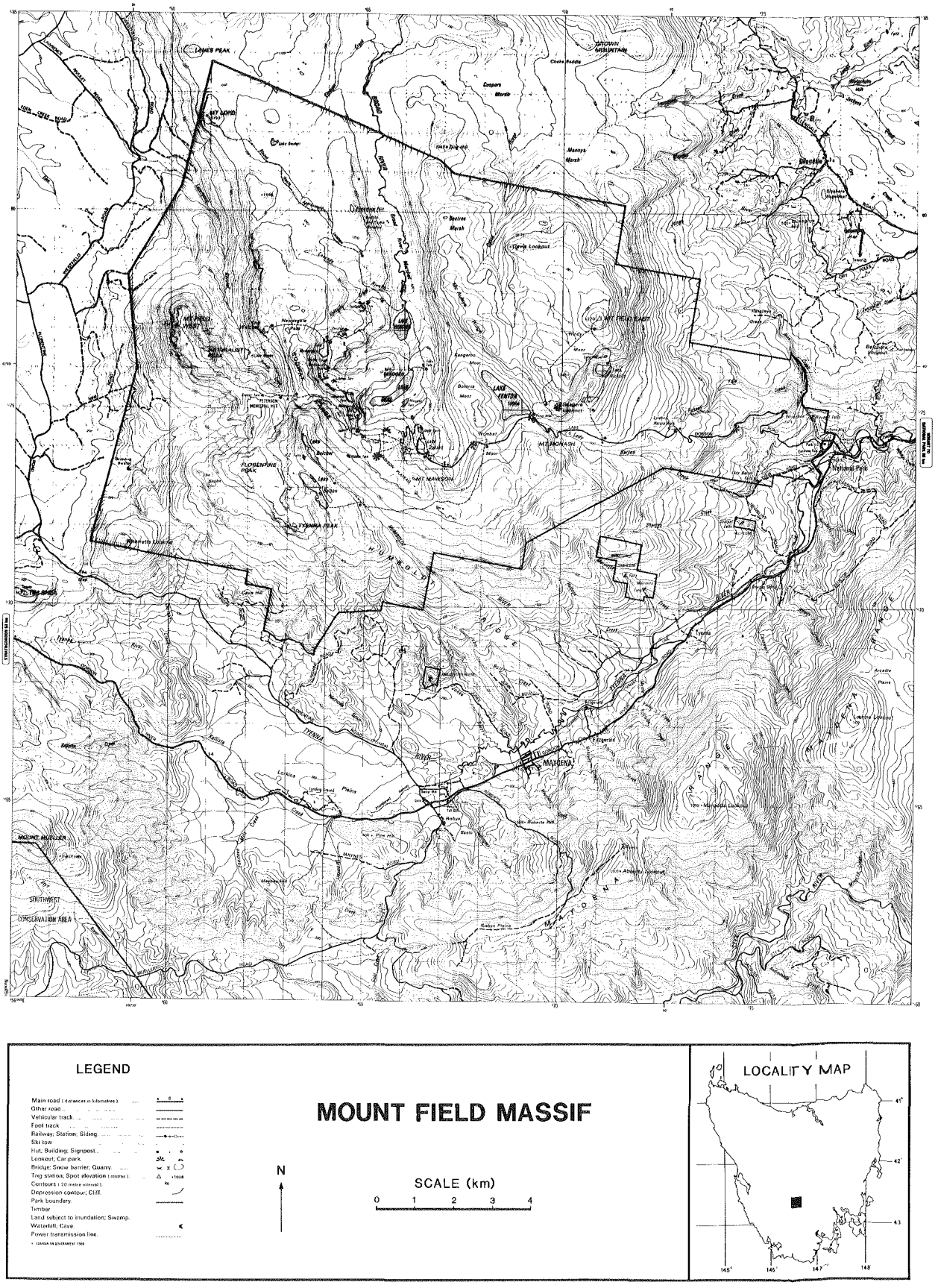
of ordination in studying compositional changes following disturbance.

This chapter provides an introduction to the physical environment and history of the study area.

6.2 Location and Topography

The Mt. Field massif is situated in south-central Tasmania at latitude 40°40'S, longitude 146°35'E, 75km WNW of the Tasmanian capital, Hobart (Figure 6.1). It is an approximately triangular, uplifted fault block surrounded by the valleys of the Derwent, Florentine and Tyenna Rivers. The west to south-western and east to south-eastern edges of the plateau are bordered by steep escarpments, whereas the northern slopes are more gradual. The roughly north-south trending glacial valley, now occupied by the Broad River, separates the undulating surface of the eastern plateau, with an average altitude of about 1070m, from the more rugged terrain to the west. The summit of the dome shaped Mt. Field East (1270m) is the highest point on the eastern side of the massif.

The western side of the plateau is so deeply dissected by the two large glacial valleys, now occupied by Lawrence Rivulet and the Humboldt River, that it consists of a system of ridges and small higher plateau surfaces, the arrangement of which approximates an inverted letter "K" (Figure 6.1). The upright of the "K" is formed by the Rodway Range (maximum altitude c.1370m), with the highest peaks on the massif, Mt. Field West (1434m), Naturalist Peak (c.1420m) and Tyenna Peak (c.1405m), being located on the other two arms of the "K". K col, which forms the


LEGEND
MOUNT FIELD MASSIF
N
SCALE (km)
0 1 2 3 4
LOCALITY MAP
MOUNT FIELD NATIONAL PARK
MOUNT MUELLER
SOUTHWEST CONSERVATION AREA
MAYDENA
TYENNA
HUNTSMAN
LAKE FENTON
LAKE DOBSON
LAKE NEWDEGATE
LAKE BINNEY
LAKE SEDGWICK
LAKE HAUY
LAKE WEBB
LAKE BELLA
LAKE SALLY
LAKE HOWARD
LAKE ADELAIDE
LAKE ANNE
LAKE HAMILTON
LAKE HOGARTH
LAKE HOLLOWAY
LAKE HOLLY
LAKE HOLMES
LAKE HOLYOAKE
LAKE HOLYROOD
LAKE HOLYWELL
LAKE HOLYWOOD
LAKE HOLYWOOD
LAKE HOLYWOOD

connection between these two ridges and the Rodway Range, takes its name from the "K" shaped configuration. The small higher plateau surfaces include the Mawson Plateau (c.1260m) and level areas near The Watcher, Florentine Peak and Naturalist Peak (Figure 6.1).

6.3 Geology and Geomorphology

The mountains of Tasmania fall into two major structural provinces (Davies 1965). In the west, elongated ridge systems predominate, while the central, eastern and south-eastern mountains are generally of plateau form. These differences reflect an underlying structural division. In the so-called fold structure province of the west, extensively folded basement rocks of pre-Carboniferous age are exposed. River systems have tended to excise valleys following the line of strike of the softer strata, leaving ridges of the more resistant rocks, such as quartz metamorphics and conglomerates. The trend of the resulting ridge systems is related to the direction of the major fold axes.

In the fault structure province of the centre, east and south-east the pre-Carboniferous rocks are overlain by more or less horizontal sediments of Permian and Triassic age, into which massive sheets and sills of dolerite were intruded during the Jurassic. Some of these sills reach 430m in thickness (Banks 1965). Faulting during the late Cretaceous or early Tertiary produced horst and graben structures. Since dolerite is relatively resistant to weathering, most of the plateaux are now dolerite capped, erosion having largely removed the overlying sediments.

Mt. Field lies on the western margin of the fault structure

province. The plateau top consists almost entirely of Jurassic dolerite, although a few small remnants of the overlying sediments occur in places. On the eastern slopes, Triassic sandstones, underlying the dolerite, are exposed. The contact occurs at an altitude of about 760m, although it is masked by a Pleistocene solifluction mantle of mostly doleritic material. The Triassic sediments rest conformably on mudstones and sandstones of Permian age. A major unconformity extends around the lower south-western and western slopes of the plateau, where the Jurassic dolerite and post-Carboniferous sediments overlie folded Ordovician rocks (principally the Gordon Limestone).

Much of the present landscape on the Mt. Field massif is dominated by glacial and periglacial features dating from the Pleistocene. Derbyshire (1972), has reviewed the available evidence concerning the Pleistocene glaciation in Tasmania. Derbyshire and Peterson (1971) consider that most of the glacial landforms in Tasmania date from the last of several distinct glacial episodes, which they correlate with the Weischel-Wisconsin glaciation in the northern hemisphere. However, K. Kiernan (personal communication 1983) has found evidence for three glacial phases at several sites in western and north-western Tasmania, the oldest of which appears to have been the most extensive. He considers that most of the largest erosional features date from this first stage. The second phase appears to have been less extensive, while the last (i.e. most recent) was apparently quite restricted.

Preliminary descriptions of some of the glacial features at Mt. Field were provided by Taylor (1922) and Lewis (1922a,b) and some aspects of the glacial geomorphology have since been considered by

Jennings and Banks (1958), Peterson (1968) and Davies (1969). However, no detailed comprehensive study has been performed. The glaciation at Mt. Field was of the "cirque and valley" type, with cirque floor levels ranging from about 900 to 1000m. A massive glacier flowed northwards for up to 9km in the valley now occupied by the Broad River, augmented by two shorter tributaries from the west. The over-deepened cirque of one of these tributaries is now occupied by Lake Seal. The floor of the Broad River Valley is covered by fluvio-glacial outwash deposits, and recessional moraines cross the valley in several places. Lake Webster is dammed by one such moraine. The origin of Tarn Shelf, a ledge about 100 to 400m wide, sloping gently to the north between the Rodway Range and the head walls of the short tributaries to the Broad River glacier, is not certain. The basins occupied by some of the tarns on the shelf appear to be ice-scoured.

West of the Rodway Range, a large glacier flowed north in the valley now occupied by Lake Hayes and Lawrence Rivulet, while another flowed south-east in the Humboldt Valley. Glaciation on the eastern side of the massif was more restricted. Two small cirques on the upper south-eastern slope of the plateau, between Seager's Lookout and Mt. Field East, were formed by small glaciers which flowed south-east and south respectively. At their greatest extent, both were apparently less than one kilometre in length. Lake Nicholls now occupies the over-deepened floor of the cirque of the south-east moving glacier, while Beatties Tarn is dammed by a moraine deposited by the south-flowing glacier. Lewis (1922a) suggested that another glacier flowed south-east from Kangaroo Moor and carved the shallow basin now occupied by Lake Fenton. However, Davies (1965) considered that Lake

Fenton probably owes its origin to damming by solifluction deposits, rather than scouring by glacial ice.

If the series of three glacial stages mentioned above (K. Kiernan, personal communication 1983) also occurred at Mt. Field, it is probable that the bulk of the erosion of the largest glacial valleys dates from the first, most extensive stage, while most of the existing depositional features belong to the final stage. Radiocarbon ages for basal sediments in several lakes and tarns on the Mt. Field plateau, reported by Macphail (1979), suggest that both Beatties Tarn, at an altitude of 990m on the eastern side of the plateau, and Eagle Tarn, some 4km to the west at an altitude of 1033m, were de-glaciated by 11400 BP. Glacial ice remained somewhat longer at higher altitudes, especially in situations sheltered from the afternoon sun. An unnamed tarn at an elevation of 1160m on Tarn Shelf, only 2.5km WNW of Eagle Tarn, was de-glaciated by 9700 BP.

On the plateau top, those areas not affected by glacial ice were subject to periglacial "freeze-thaw" processes which may have operated down to an altitude as low as 450m (Davies 1965). It is likely that the glaciated areas were also subject to a periglacial regime for some time following de-glaciation. A solifluction mantle of mostly doleritic material covers large areas on the plateau top and extends down the upper slopes of the plateau. In these deposits, sub-rounded dolerite boulders up to 1.5m across generally occur in a surface layer. Below the boulders, clay-loam or sandy clay-loam, containing numerous rock fragments (often aligned parallel with the surface), may extend to a depth of several metres. Frost-shattering has produced screes of

angular dolerite boulders below many of the steeper outcrops. At the highest altitudes, some frost-wedging probably still occurs.

The geomorphological regime during the Holocene has been predominantly fluvial. The major streams draining the plateau are the Broad River to the north, Lawrence Rivulet to the north-west, the Humbolt River to the south-east and Lady Barron and Russell Falls Creeks to the east.

6.4 Soils

The reconnaissance survey of Dimmock (1961) is the only available study of the soils on the Mt. Field Plateau. He recognised two major soil types for the purpose of mapping. These were the yellow-brown soils (Ybs) of moderate to well drained areas on the upper slopes and the plateau top, and high moor peats (HMP), developed in situations of impeded drainage on the plateau top. Both soils are generally associated with Pleistocene solifluction or glacial deposits.

The yellow-brown soils display a range of profiles, depending on drainage conditions. In the wetter situations, a shallow peaty surface overlies an olive coloured compact loam or sandy loam and a thin, reddish iron pan generally occurs at a depth of 30 to 45cm. The iron pan forms an effective barrier to water and roots. In road cuttings, water may often be observed weeping from just above the iron pan. The perched water table resulting from the presence of the pan is of undoubted ecological significance. Below the iron pan is an horizon of friable clay- loam or sandy clay-loam with a strong brown colour. This horizon may sometimes extend to a considerable depth. In better-drained

situations, the peaty surface is replaced by a friable, highly organic loam or clay-loam and the iron pan is absent.

Dolerite fragments of various sizes are common throughout the profile, with the largest boulders generally occurring in the surface 60cm. The physical analysis of a profile (serial number H240), sampled by Dimmock (1961) in his reconnaissance survey, showed that rocks and gravel comprised between 40 and 55% of the profile. Texture is fairly uniform within a given profile, but may vary between different profiles, from predominantly clayey or silty to predominantly sandy throughout.

The high moor peats, developed under conditions of impeded drainage, are essentially similar to the yellow-brown soils, except for a greater thickness of peat at the surface. The peat is often between 30 and 40cm in depth. It is acid (pH 5 to 5.5) and often exceeds 50% organic matter in the surface 30cm.

The range of soils developed on the solifluction deposits may be regarded as a catena, essentially related to drainage conditions. The catena extends from yellow-brown soils on well drained sites, through peaty yellow-brown soils with iron pan development in moderately drained situations, to high moor peats on the most poorly drained sites.

Dimmock (1961) did not describe the soils developed on those parts of the plateau top where solifluction deposits are absent. Such areas include most of the terrain above an altitude of c.1220m and numerous rocky outcrops below that altitude. Soils in these situations have usually developed *in situ* since de-glaciation. They are generally shallow and skeletal. In well drained situations, rocky lithosols occur, with little profile development except for some accumulation of

humus near the surface. These soils may be as shallow as 2cm and they rarely exceed 10cm in depth. Where drainage is impeded, a surface layer of highly organic, acid peat develops. Analyses of bulked samples of the surface 5cm of such peats (Kirkpatrick, Dickinson and Cantle 1982; N. Gibson, personal communication 1983) show a range in pH from 4 to 6.5, with a mean of 5.5. The percentage of organic matter often exceeds 50% and may be as high as 90%. Approximate ranges of concentration (ppm) for selected mineral nutrients are as follows: total phosphorous 100-500; water soluble nitrogen 80-140; potassium 60-240; sodium 40-300; and calcium 220-2000. The peats are generally shallow, ranging from 2 to 20 cm in thickness, although peats exceeding 100cm in depth occur in string bogs, associated with damming by cushion-plant species (Kirkpatrick and Gibson 1983).

6.5 Climate

6.5.1 General

The climate of Tasmania is essentially temperate in character, although the maritime influence, resulting from the relatively small size of the island, gives rise to abnormally mild winters and cool summers for these latitudes (41-43°S). It is broadly controlled by the meandering westerly wind regime, characteristic of the latitudes 40-60°S, and colloquially known as the "roaring forties". Langford (1965) has described the main features of the general circulation and outlined the weather patterns associated with some typical synoptic situations. In summer, the northern fringe of the westerlies is generally located south of Tasmania and the average path of anticyclones extends from west to east just north of the island. During winter, the

westerly wind belt extends across Tasmania and the average path of anticyclones is displaced northwards across the Australian continent. At times, cyclones break away from the westerly wind belt and move across south-eastern Australia to intensify in the Tasman Sea. When this occurs, an anticyclone develops concurrently from a ridge of high pressure south of the Australian Bight and generally moves eastwards across, or just south of Tasmania.

The predominantly westerly direction of rain-bearing winds produces a marked precipitation gradient from west to east across both individual mountains and the island as a whole. Mt. Field Plateau lies on the boundary between the per-humid and humid precipitation-effectiveness provinces described by Gentilli (1972). The only permanent weather station located on the plateau is a rain gauge at Lake Fenton (altitude 1010m), and the nearest comprehensive station is near Maydena, some 9km south of the plateau (altitude 267m). Rainfall records are also available for several stations surrounding the massif.

6.5.2 Wind

Wind direction diagrams for Maydena, based on 17 years of daily observations at 3 p.m. (Figure 6.2), clearly illustrate the predominance of west to south-westerlies throughout the year. Calm conditions are most frequent in the months June to August. Another notable trend is an increase in the frequency of north-east to north-westerlies in the summer months (December to February). Wind speed data (Table 6.1) show that the frequency of occurrence of wind speeds between 6 and 30 km/hr is greatest in spring, followed (in decreasing order) by summer, autumn and winter. For wind speeds of 5

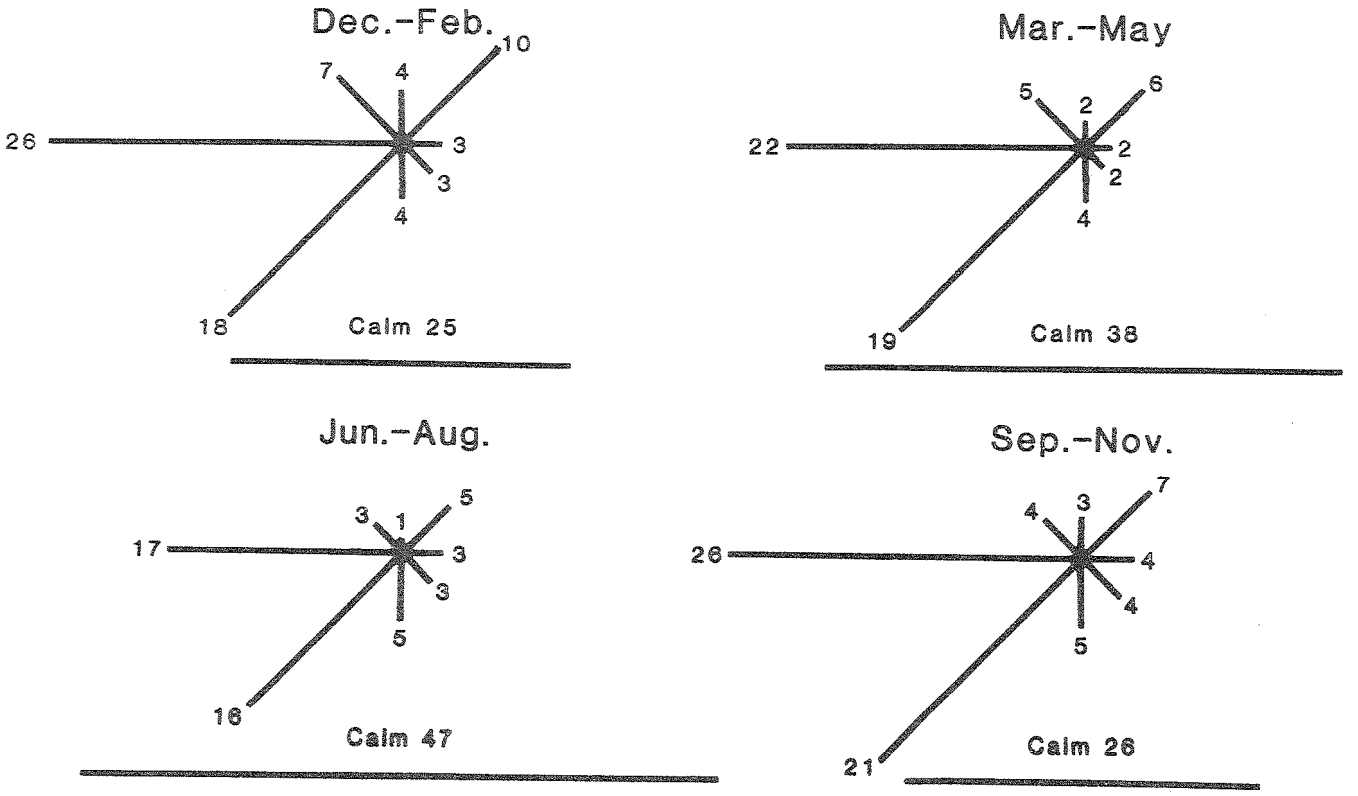


Figure 6.2 Wind direction diagrams for the Maydena station, which is located about 7 km south of the study area, at an altitude of 267 m (see Figure 6.4). The length of each bar is proportional to the percentage of days on which the wind blows from the indicated direction during each three month period. Percentage figures are given at the end of each bar. The length of the horizontal bar below each diagram similarly represents the percentage of calms. The figures are based on 17 years of daily observations at 3 p.m. (1965-1981), and they were computed from monthly frequencies supplied by the Bureau of Meteorology, Hobart.

Wind Speed (km/hr)	Frequency of Occurrence (%)			
	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Calm	25	38	47	26
1 - 5	15	19	18	14
6 - 10	29	24	21	27
11 - 20	17	12	10	21
21 - 30	9	5	3	9
31 - 40	3	2	1	3
41 - 50	1	+[1]	+	+
>50	1	+		+

[1] + = observed, but with a frequency less than 0.5%.

Table 6.1 Wind speed frequencies for Maydena, based on 17 years of daily observations at 3 p.m. (1965-1981). Adapted from data supplied by the Bureau of Meteorology, Hobart.

km/hr or less the sequence is reversed, with winter having the highest frequency and spring the lowest. Wind speeds greater than 30 km/hr are fairly infrequent throughout the year, although not so rare as these spot observations at 3 p.m. suggest. An examination of the joint frequency distribution of wind observations in relation to direction and speed, revealed that the highest speeds are generally associated with west to south-westerlies at all times of the year.

On the plateau, the speed and persistence of the wind is likely to increase with altitude. During field work, which was mostly performed in the months December to April, winds of sufficient strength to make walking difficult were often encountered, especially in the higher altitude situations exposed to the west and south-west (e.g. Mawson Plateau). In such situations, "wind pruning" of shrubs and their greater development on the east to north-east side of boulders, clearly indicate the prevailing wind direction.

Severe west to south-westerly gales, with mean wind speeds greater than 60km/hr and gusts of more than 100km/hr, may occur at any time of the year. They are usually accompanied by heavy precipitation, which may be in the form of sleet or hail, especially at elevations above about 1000m. The effect of these strong, ice-bearing winds on woody vegetation is likely to be most severe in late summer, when new growth has not yet been hardened. A lack of predictably favourable conditions for growth in the summer months, due to these occasional glazing storms, is a characteristic feature of the climate on Mt. Field Plateau, and Tasmanian mountains in general.

6.5.3 Precipitation

Since the predominant direction of rain-bearing winds is west to south-westerly, one would expect a precipitation gradient across the Mt. Field massif (aligned approximately WSW to ENE), superimposed upon a general increase in precipitation with altitude. Figure 6.3 shows the average annual rainfall at several stations in the vicinity of the plateau. These figures are broadly consistent with such a generalisation.

Monthly rainfall data for Lake Fenton are given in Table 6.2, the averages being based on 44 years of observations. Mean annual rainfall is 1553mm. This is distributed fairly evenly throughout the year. The driest three month period is January to March, with an average of 18.4% of the annual total, and the wettest is July to September (28.5%). The lowest rainfalls ever recorded for each month vary from 15 to 37% of their respective averages, while the highest recorded monthly rainfalls range from 160 to 331% of average. The lowest recorded rainfalls for the months December to March range from 19 to 31mm, indicating that reasonably dry conditions occasionally prevail during summer.

In exceptionally dry summers, normally waterlogged peats may dry out sufficiently, at least at the surface, to support fire. The lowest monthly rainfall recorded at Lake Fenton (19mm) was in December 1960. Early in 1961, a wild-fire, accidentally started by fishermen near Lake Belton, burnt out most of the Humboldt Valley and extended onto the south-western edge of Mawson Plateau. Up to 20cm of peat was burnt in some places. In addition to increasing the susceptibility of subalpine and alpine vegetation to fire, occasional dry spells during summer may

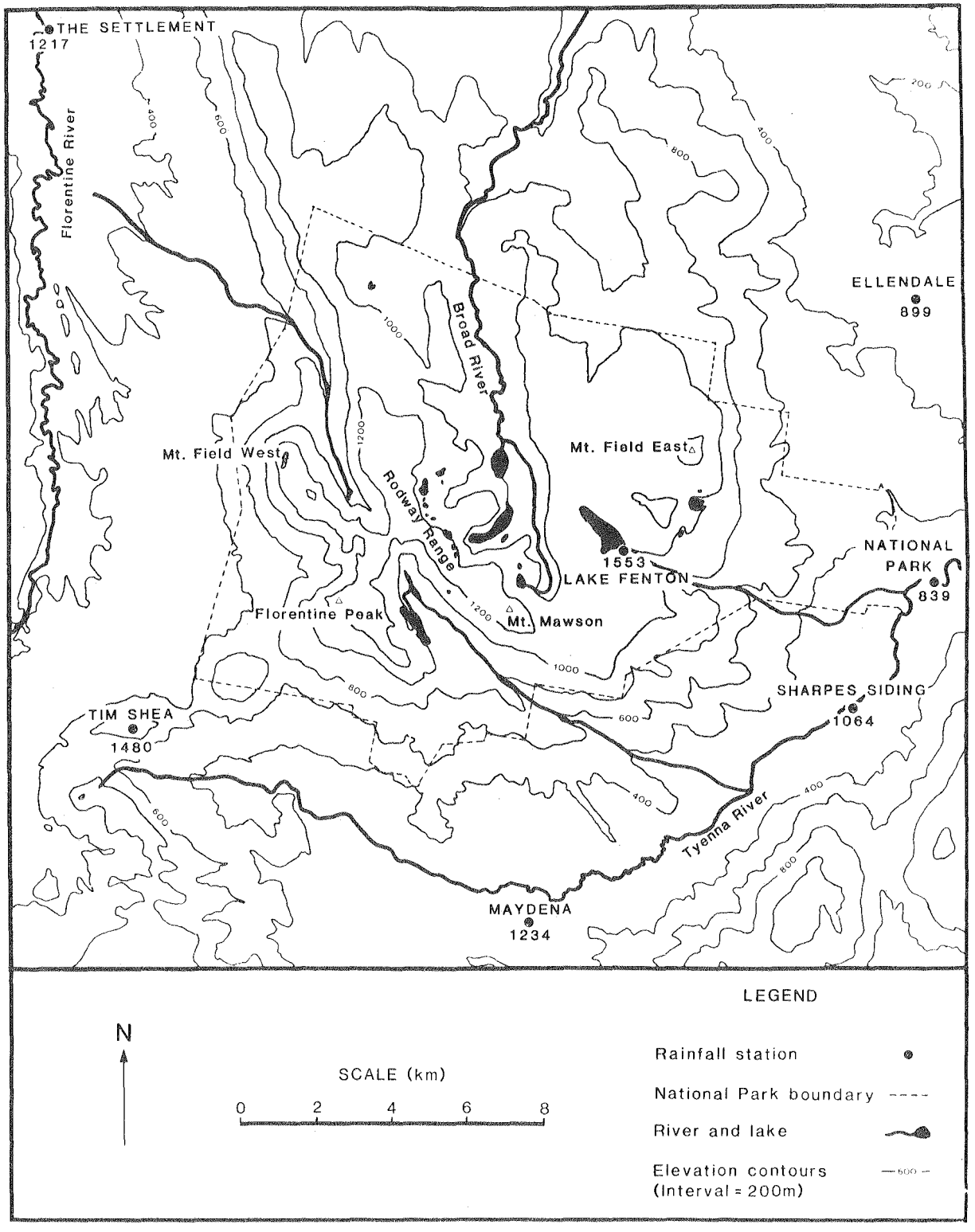


Figure 6.3 Map of the Mt. Field massif and surroundings, showing the location of long-term rainfall stations and their mean annual rainfalls. Rainfall data were supplied by the Bureau of Meteorology, Hobart, and the elevation contours and other details were copied from 1:100000 scale maps of the area produced by the Lands Department. Observation periods for the rainfall averages were as follows: The Settlement 23 years, 1957-1982; Tim Shea 26 years 1955-1982; Maydena 28 years, 1952-1982; Sharpes Siding 69 years; National Park 22 years; Lake Fenton 42 years, 1938-1982; Ellendale 39 years, 1901-1940.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean rainfall (mm)		89	93	104	137	146	131	143	149	151	142	142	126	1553
Median rainfall (mm)		81	82	94	130	135	116	131	144	146	142	130	124	1550
Mean rainfall as a percentage of annual mean	Monthly	5.7%	6.0%	6.7%	8.8%	9.4%	8.4%	9.2%	9.6%	9.7%	9.2%	9.2%	8.1%	
	3-Monthly		18.4%			26.6%			28.5%			26.5%		
Lowest recorded rainfall (mm)		30	20	31	45	48	34	43	39	45	53	35	19	981
Percentage of mean value		34%	22%	30%	33%	33%	26%	30%	26%	30%	37%	25%	15%	63%
Highest recorded rainfall (mm)		175	270	208	303	459	434	366	272	242	282	353	286	2107
Percentage of mean value		197%	290%	200%	221%	314%	331%	256%	183%	160%	199%	249%	227%	136%

Table 6.2 Rainfall data for Lake Fenton, based on 44 years of observations from 1938 to 1982. Data supplied by the Bureau of Meteorology, Hobart.

be a limiting factor for some species, especially on well drained sites and boulderfields.

Monthly median rainfalls are generally lower than the means (Table 6.2), indicating that monthly falls less than the mean are more common than those greater than the mean. However, this skewness does not apply to the annual totals, where the mean and median are virtually identical. The annual totals deviate from the average by only c.36%. This suggests that periods of exceptionally high or low rainfall are generally of short duration.

In order to obtain some estimate of the rainfall on other parts of the Mt. Field plateau, six rain gauges were installed in November 1981 and read at approximately two-weekly intervals until April 1982. The gauges had a galvanised iron funnel, with a rim diameter of 28cm, and a plastic collecting tank with a capacity of 25l (400mm of rainfall). The vertical height of the funnel rim was 5cm and the slope of the base of the funnel was 26°. Earlier trials in the 1980-1981 summer, with standard 12.7cm (=5 inch) funnels, indicated considerable variability between readings from adjacent gauges. This variability was greatly reduced when the larger funnels were employed. Another advantage of the larger collecting surface is that a greater volume of water is collected. Thus the proportional error in measuring the volume tends to be less. The locations of the gauges are indicated in Figure 6.4. The stations were positioned so as to cover the range of altitude from 980m to 1300m. Monthly rainfall totals for the period December 1981 to March 1982 are given in Table 6.3, together with the contemporaneous data for Lake Fenton. The two highest altitude stations (5 and 6) consistently

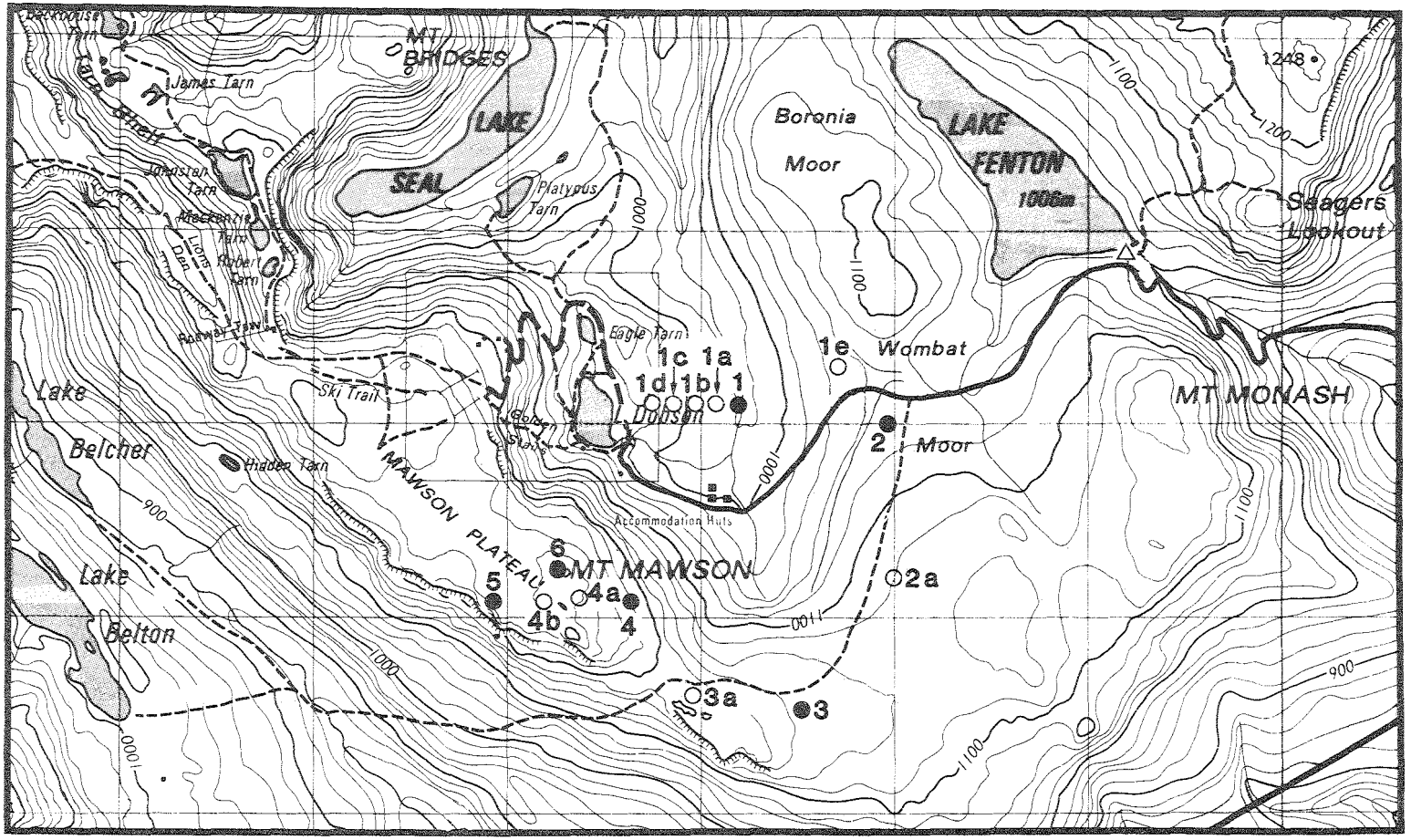


Figure 6.4 Map of the study area, showing the locations of the temporary weather stations established on the plateau top. Solid circles (●) indicate stations comprising a maximum-minimum thermometer, a rain gauge and a towelling evaporimeter, while open circles (○) mark the positions of stations consisting of a thermometer only. The permanent rain gauge located near the south-east corner of Lake Fenton is indicated by an open triangle (△). Numbering of the stations accords with the system used in the text and in Tables 6.3, 6.5, 6.7 and 6.8. The map is reproduced from the 1:50000 scale sheet of Mt. Field National Park with the permission of the Lands Department.

Station	Altitude (m)	Distance ENE of station 4 (km)	Rainfall (mm) Dec.1981	Jan.1982	Feb.1982	Mar.1982	Four Month Total	Estimated Averages Dec.-March	Annual
Lake Fenton	1010	3.2	101	56	51	128	336	412[1]	1553[1]
2	1070	1.6	123	85	113	119	440	538	2030
1	980	0.9	168	92	106	107	473	580	2190
3	1150	0.7	153	91	119	125	488	599	2260
4	1220	0.0	178	110	145	130	563	689	2600
5[2]	1280	-	110	69	90	96	365	-	-
6[2]	1300	-	51	56	43	84	262	-	-

[1] Actual averages based on 44 years of observations (see Table 6.2).

[2] Excluded from consideration, since low readings are probably an artifact due to wind exposure.

Table 6.3 Rainfall data for the six stations established on the Mt. Field Plateau, together with the contemporaneous readings at Lake Fenton. Four monthly and annual averages were estimated for stations one to four on the assumption that the proportional departure from average of the four month totals for each station was identical to that at Lake Fenton during the observation period. Lake Fenton data were supplied by the Bureau of Meteorology, Hobart. The locations of the stations are shown in Figure 6.4.

recorded the lowest rainfalls. Both were located in wind-exposed situations on Mt. Mawson. It is highly probable that the low readings are an artifact, related to turbulence in the vicinity of the funnels. Hence the data from these stations will not be considered further. The accurate measurement of rainfall in exposed alpine areas probably requires special instrumentation.

The four month totals for the remaining stations were compared with the total for the same period at Lake Fenton. The long term average for Lake Fenton for the months December to March is 412mm, 26.5% of the annual average (Table 6.2). The rainfall for December 1981 to March 1982 was 336mm, 81.5% of the average for these four months. On the assumption that these percentages are generally applicable for that region of the plateau in which the rain gauges were located, average December-March and annual rainfalls for stations 1 to 4 were computed (Table 6.3). These are only regarded as crude estimates.

When the annual rainfall estimates were plotted on a map showing the locations of the stations, a monotonic decrease in rainfall from Mt. Mawson to Lake Fenton was apparent. In order to investigate this trend more precisely, co-ordinates for each station on an axis bearing ENE from Mt. Mawson were obtained by perpendicular projection. Station 4 was taken as the arbitrary origin. A scatter plot of estimated rainfall v. co-ordinate along this axis was prepared (Figure 6.5). The plot suggested a linear relationship between rainfall and distance ENE of Mt. Mawson. A linear regression of rainfall (R) on ENE co-ordinate (X) gave the equation $R = 2525 - 311.4X$, with the fitted model accounting for 98% of the variance of R. The observations thus suggest an approximately linear decline in rainfall from Mt. Mawson to Lake

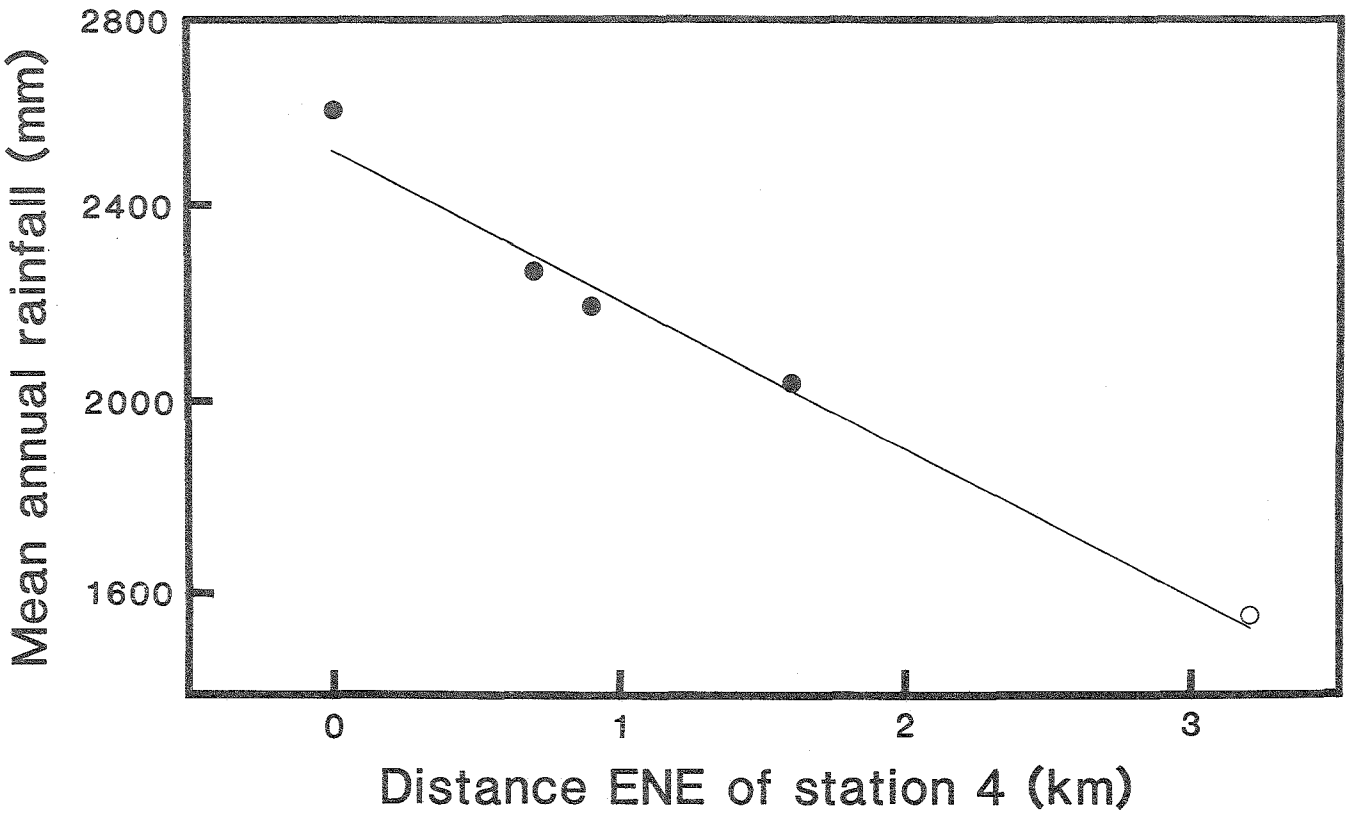


Figure 6.5 Scatter diagram illustrating the relationship between mean annual rainfall at stations 1-4 and Lake Fenton and distance ENE of station 4. The mean rainfall figures for stations 1-4 (●) are estimates, the derivation of which is explained in the text, while the figure for Lake Fenton (○) is based on 42 years of records. The fitted linear regression of rainfall on distance accounts for 98% of the rainfall variance.

Fenton, the rainfall at Lake Fenton being only 60% of that on the upper eastern slopes of Mt. Mawson.

The annual rainfall estimate of 2600mm for station 4 is considerably higher than the figure of 2030mm postulated by Gilbert (1959) for the highest parts of the plateau. It is probable that rainfall on Mawson Plateau and the more elevated areas to the west (e.g. Rodway Range, Naturalist Peak and Tyenna Peak) is even greater than 2600mm. It is also likely that the region of the plateau ENE of Lake Fenton has an annual rainfall less than the 1553mm received at Lake Fenton.

From June to September, most of the precipitation at altitudes greater than about 1000m falls as snow, or occasionally hail. Although snowfalls may occur in any month, the major falls generally occur from late May to late August. Prolonged, extensive snow cover is a rarity on the Mt. Field Plateau, as it is on Tasmanian mountains in general (Kirkpatrick 1983). This is due to the maritime influence, which results in relatively mild winter temperatures, and the occurrence of spells of warm, sunny weather in mid-winter. At elevations above 1200m, the maximum duration of extensive snow cover is probably about three months. Snow patches in topographically sheltered situations, on the north-east to south-east side of ridges, may persist until January. In suitable places, the formation of snow patches is an annual event and a distinctive vegetation pattern may result (e.g. Gibson and Kirkpatrick 1983).

Edwards (1973) found that "mist stripping" by vegetation significantly augmented other forms of precipitation on the Central

Plateau, Tasmania. It is likely that this phenomenon also occurs on the Mt. Field Plateau.

6.5.4 Evaporation

Evaporation data for Maydena are given in Table 6.4. Mean annual evaporation is 724mm, which is 59% of the mean annual rainfall. Mean monthly evaporation varies from 127mm in January to 15mm in June, significantly exceeding mean monthly rainfall only in January and February. Variation in the evaporation for a particular month from year to year, as reflected by the extreme observations given in Table 6.4, is not great. On the plateau, evaporation in all months is likely to increase with increasing altitude, due mainly to an increase in wind speed with altitude. In addition, insolation on the plateau top is probably greater than in low-lying situations such as Maydena, since elevated regions are unaffected by valley fogs. Fogs are fairly common at Maydena, especially in the winter months (Table 6.4), and they often persist until midday.

During the 1981-1982 summer, an attempt was made to obtain a measure of relative evaporation at the same six stations on the plateau top for which rainfall data were presented in section 6.5.3. The use of standard open-pan evaporimeters was not practicable. Daily supervision would have been necessary, due to the high rainfall, and problems with interference by native mammals and birds were anticipated. Accordingly, an instrument was designed in which water was evaporated from a strip of towelling, which drew water by capillary action from a closed reservoir (Figure 6.6). The towelling wick entered the lid of the reservoir through two narrow slits which were surrounded by a rim, preventing

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean rainfall (mm)		58	59	72	112	128	109	124	129	124	110	109	100	1234
Median rainfall (mm)		57	53	69	109	112	103	105	134	130	111	91	88	1207
Mean number of rain days		12	11	14	18	20	18	21	21	19	19	18	17	208
Mean evaporation (mm)		127	107	71	42	25	15	16	28	42	65	84	102	724
Lowest recorded evaporation (mm)		96	82	50	30	16	9	9	22	36	47	72	87	
Highest recorded evaporation (mm)		183	138	96	63	65	42	28	40	60	78	105	118	
Mean hours of bright sunshine per day		6.8	6.2	5.0	3.5	2.9	1.8	2.2	3.3	3.6	4.7	5.2	5.7	
Mean relative humidity at 9am (%)		71	76	79	86	91	92	92	90	80	75	72	70	
Mean relative humidity at 3pm (%)		49	50	57	68	76	79	78	72	62	59	55	55	
Mean number of clear days		4	4	3	1	1	1	1	1	1	2	2	2	
Mean number of cloudy days		12	11	15	18	20	20	21	20	19	17	16	16	
Mean number of days on which phenomenon was observed	Snow	0	0	0	0	1	1	1	2	1	1	0	0	
	Frost	1	1	2	2	7	9	11	12	10	7	3	2	
	Mist/Haze	3	3	4	4	2	4	3	4	2	3	3	2	
	Fog	1	1	2	4	8	8	8	6	2	1	0	0	

Table 6.4 Climatic data for Maydena supplied by the Bureau of Meteorology, Hobart.
The number of years of observations and the periods covered are as follows: rainfall 31 yrs, 1952-1982; evaporation 15 yrs., 1968-1982; sunshine 14 yrs., 1966-1979; humidity 31 yrs., 1952-1982; phenomena 18 yrs., 1965-1982.

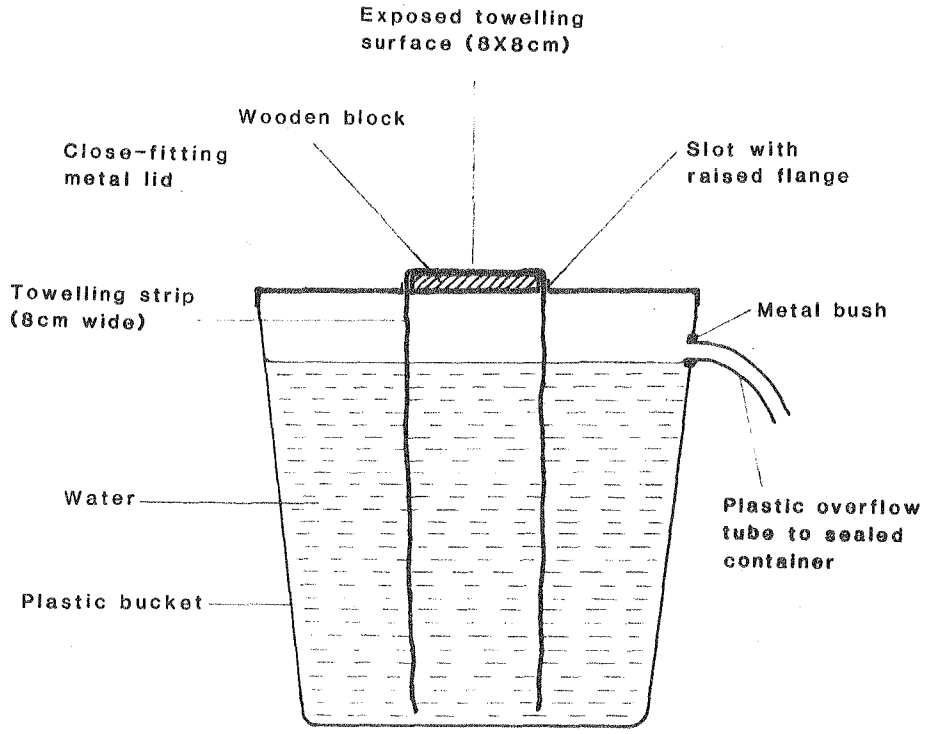


Figure 6.6 Diagrammatic cross-section of the towelling-wick evaporimeter used to obtain a measure of relative evaporation at six stations on the Mt. Field Plateau.

rainwater or dew collecting on the lid from flowing into the reservoir. Nevertheless, trials during the 1980-1981 summer showed that a significant amount of rain was able to enter the reservoir, presumably by super-saturating the towelling and reversing the capillary flow. Accordingly, an overflow tube leading to a sealed, container was installed to prevent the water in the reservoir rising above a certain level. The instruments were initially set up by saturating the towelling and filling the reservoir with water up to the lip of the overflow outlet. Subsequently, they were read by recording the volume of water necessary to bring the level back up to this mark and the volume of water (if any) in the overflow collector.

If V is the volume of water added to bring the level in the reservoir back up to the lip of the overflow outlet, O is the volume of water in the overflow collector and R is the volume of rain water which has entered the reservoir, then the net evaporative loss is given by V+R-O. Although rainfall data are available for each station, the relationship between the rainfall and the volume of water entering the reservoir of the evaporimeters is not known precisely. This could only be established by detailed experiments. It is probable that the proportion of rain entering the reservoir would vary with the intensity of the rainfall and the wind speed. During heavy falls, splashing would be expected to occur, both from the metal lid of the evaporimeter onto the towelling and in the opposite direction. It is not known whether these two processes would balance each other. Nevertheless, in order to obtain some estimate of R, the crude assumption was made that the volume of rain entering the reservoir was equal to the theoretical volume falling on an area of $64cm^2$, this being the area of the towelling

exposed on the top of the evaporimeter. For stations 5 and 6, where rainfall readings were suspisciously low (see section 6.5.3), the contemporaneous rainfall data for station 4 were used.

The resulting monthly estimates of net evaporative loss are given in Table 6.5, along with information on the altitude, topographic position and inferred wind exposure of the stations. The numbering of the six stations accords with Figure 6.4. In view of the various practical difficulties involved in deriving these figures, attempts to interpret any but the grossest variation would be unwise. The major point to be noted is that estimated evaporative loss at station 6 was usually much greater than at the other stations. The four-month total for station 6 is approximately twice that obtained at the remaining stations. Variation among the other five stations is relatively small, with rank order showing no consistent trend from month to month. Despite a considerable range in altitude (980 to 1280m) and perceived wind exposure, the four-monthly evaporation totals for these five stations are similar. Evaporation, as estimated by these instruments, thus displays considerably less variation among stations than does rainfall. The gross difference in estimated evaporation between stations 5 and 6, which were both located on exposed peaks at approximately the same altitude, suggests that differences in wind speed (due to micro-topographical features such as boulders) may have had a marked effect on the performance of the evaporimeters. With the exception of the December estimate for station 4, evaporation during January and February was considerably greater than in December and March at all stations. This is consistent with the January-February maximum in pan evaporation at Maydena (Table 6.4).

Station	Altitude (m)	Topographic Position	Regional Slope (°)	Aspect	Inferred Wind Exposure	Net Evaporative Loss (l)				
						Dec.1981	Jan.1982	Feb.1982	Mar.1982	Four Month Total
1	980	Valley bottom	1	N	Moderate	0.60	2.64	2.38	0.67	6.29
2	1070	Gently sloping moorland	2	NW	Mod.-High	1.27	2.37	2.31	0.81	6.76
3	1150	Gently sloping moorland	2	N	Mod.-High	0.88	2.20	1.77	0.22	5.07
4	1220	Upper slope	15	E	High	2.97	1.96	1.33	0.49	6.75
5	1280	Peak	0	-	Extreme	1.44	2.19	2.28	0.76	6.67
6	1300	Peak	0	-	Extreme	1.92	3.82	4.07	1.82	11.63

Table 6.5 Evaporation data for the six stations established on the Mt. Field Plateau. The locations of the stations are shown in Figure 6.4.

6.5.5 Temperature

Temperature data for Maydena, based on 17 years of records, is given in Table 6.6. The warmest month is February, with a mean daily minimum of 8.8°C and a mean daily maximum of 22.1°C, and the coldest is July, with a mean daily minimum of 1.5°C and a mean daily maximum of 9.6°C. Also presented in Table 6.6 are the mean values (over 17 years) of the lowest and highest daily minimum and the lowest and highest daily maximum observed during each month. These figures are indicative of the considerable daily variation which may be expected in all months. For example, in February the highest daily maximum averages 36.8°C while the lowest daily minimum averages 0.0°C. The corresponding figures for July are 18.7°C and -6.1°C.

The number of days with minima less than 0°C varies from a mean of zero in the months December to nine in July and August, but shows considerable variation from year to year, as indicated by the lowest and highest recorded frequencies for each month (Table 6.6). At the other extreme, the number of days with a maximum temperature exceeding 30°C averages three in January, but is zero from April to October.

All the abovementioned data refer to temperatures measured inside a standard Stevenson screen. Data on daily terrestrial minima, measured close to the ground surface using a grass-minimum thermometer, are also available for Maydena (Table 6.6). The mean daily terrestrial minimum varies from 5.9°C in February to -0.5°C in August. The 17 year averages of the lowest daily terrestrial minima observed in each month, vary from -3.9°C in February to -9.4°C in June. The mean number of days on which

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean daily minimum (°C)		8.3	8.8	7.2	5.6	3.6	2.1	1.5	1.8	3.2	4.4	6.2	7.5	5.0
Mean lowest daily minimum (°C)		-3.3	0.0	-1.3	-2.5	-3.4	-6.3	-6.1	-4.4	-4.4	-3.9	-1.5	-1.0	
Mean highest daily minimum (°C)		5.0	5.6	3.9	1.7	1.7	-0.5	-1.1	-1.0	-0.2	1.5	2.3	3.5	
Mean daily maximum (°C)		21.9	22.1	19.4	15.8	12.7	10.0	9.6	11.1	13.1	15.7	17.4	19.4	15.7
Mean lowest daily maximum (°C)		28.1	27.8	24.5	18.9	15.4	12.6	11.7	13.2	15.3	19.9	22.2	26.1	
Mean highest daily maximum (°C)		37.0	36.8	35.6	27.2	22.2	17.7	18.7	22.1	25.4	28.6	35.0	35.0	
Number of days with minimum <0°C	Mean	0	0	0	1	4	8	9	9	5	3	1	0	
	Lowest	0	0	0	0	0	1	4	3	1	0	0	0	
	Highest	3	1	2	3	10	18	15	14	11	8	3	3	
Number of days with maximum >30°C	Mean	3	2	1	0	0	0	0	0	0	0	0	1	
	Lowest	0	0	0	0	0	0	0	0	0	0	0	0	
	Highest	7	5	2	0	0	0	0	0	0	0	2	5	
Mean daily terrestrial minimum (°C)		5.6	5.9	4.8	3.6	2.0	0.6	0.1	-0.5	0.9	1.9	3.9	5.2	2.8
Mean lowest daily terrestrial minimum (°C)		-7.8	-3.9	-5.0	-7.2	-6.7	-9.4	-8.9	-8.3	-6.0	-7.2	-5.5	-5.0	
Number of days with terrestrial minimum <-0.9°C	Mean	1	1	2	3	6	10	11	13	9	7	3	2	
	Lowest	0	0	0	0	1	3	5	6	5	3	0	0	
	Highest	6	3	8	10	13	15	17	22	14	12	8	6	

Table 6.6 Temperature data for Maydena (altitude 267 m) based on 17 years of daily observations from 1965 to 1982.
Data supplied by the Bureau of Meteorology, Hobart.

the terrestrial minimum was less than -0.9°C varies from one in February (with a range of zero to three) to 13 in August (with a range of six to 22). Thus frosts may occur throughout the year, but are most frequent from June to September (Table 6.4).

The environmental lapse rate has not been accurately determined at Mt. Field, although some preliminary observations of Ogden and Powell (1979) suggest lapse rates of about 5.7°C per 1000m for minimum temperatures and 10.0°C per 1000m for maxima in December to January. M. Nunez (personal communication 1983) has studied the lapse rate on Mt. Wellington in south-eastern Tasmania (latitude 42°54'S, longitude 147°14'E), using daily observations of maximum and minimum temperatures for a continuous twelve month period. His results indicate a mean lapse rate of 4.6°C per 1000m for minima and 8.3°C per 1000m for maxima. Lapse rates showed some seasonal variation. For example, lapse rates for minima and maxima were 5.0°C per 1000m and 8.7°C per 1000m in January, compared with 4.2°C per 1000m and 7.9°C per 1000m respectively in July.

Within the study area on the Mt. Field Plateau, some altitudinal variation in temperatures would be expected between the general level of the eastern plateau surface at about 1070 m and the higher peaks. In addition, it might be anticipated that cold air drainage would result in the occurrence of the most severe frosts in the valley bottoms. It has been suggested (Kirkpatrick 1983) that the lack of extensive, protracted snow cover on Tasmanian mountains may increase the ecological significance of extreme winter temperatures.

In order to gain some information about temperatures on the

plateau, 15 maximum/minimum thermometers were deployed. Their locations are indicated in Figure 6.4. The thermometers were attached to 60 X 10 X 2.5cm wooden pegs, sharpened at one end. These were driven into the ground, such that the flat surface bearing the thermometer faced south. Strips of plywood, attached to each side of the pegs, shielded the thermometers from direct solar radiation. The thermometer bulbs were 10cm above the ground surface. The structure of the vegetation at these stations varied from open-heath to low shrubland (Table 7.2) and the thermometers were placed at least one metre from the nearest erect shrub. Calibration curves for each thermometer (over the range -35°C to +40°C) were determined in the laboratory, prior to their installation at Mt. Field. Readings were estimated to the nearest 0.1°C, but the final calibrated values were rounded to the nearest 0.5°C.

In order to investigate the postulated gradient in minimum temperatures, due to cold air drainage, a transect of five thermometers was employed. The stations were spaced 110m apart, extending from near the top of the ridge east of Lake Dobson to the bottom of the upper Broad River Valley (Figure 6.4). The uppermost station (1d) was at an altitude of 1010m, while the lowest (station 1), was at an altitude of 980m. The transect was installed on 12 February 1981. However, readings from February to April 1981 were sporadic, because several field trips were prevented by inclement weather. Between 2 December 1981 and 16 April 1982, the thermometers were read at approximately two-weekly intervals. The minimum temperatures are given in Table 6.7. The thermometers were also read during a field trip on 30 June 1982 and the minimum temperatures for the 76 day period since the previous reading on

Station	Approximate elevation above valley bottom (m)	Minimum Temperature (°C)									
		2/12/81 to 17/12/81 (15 days)	18/12/81 to 31/12/81 (14 days)	1/1/82 to 13/1/82 (13 days)	14/1/82 to 29/1/82 (16 days)	30/1/82 to 12/2/82 (14 days)	13/2/82 to 4/3/82 (21 days)	5/3/82 to 17/3/82 (14 days)	18/3/82 to 31/3/82 (15 days)	1/4/82 to 16/4/82 (16 days)	17/4/82 to 30/6/82 (76 days)
1d	30	-0.5	-2.0	-2.0	0.0	-2.0	-1.0	0.0	1.0	-1.0	-9.0
1c	18	-0.5	-1.5	-2.5	-0.5	-2.5	-2.5	0.5	0.5	-1.0	-9.0
1b	8	-1.5	-2.0	-3.5	-2.0	-3.0	-3.5	-0.5	0.5	-2.5	-9.5
1a	4	-1.5	-2.5	-4.0	-3.0	-3.5	-4.0	-0.5	-1.0	-3.5	-10.5
1	1	-2.0	-1.0	-3.0	-3.0	-3.0	-4.0	-1.0	-1.0	-3.5	-11.0

Table 6.7 Minimum temperatures recorded along a transect in the upper Broad River valley. Station 1d was located about 150 m east of Lake Dobson and the others were spaced about 120 m apart along a line running due east to the valley bottom. Locations of the stations are shown in Figure 6.4

16 April are also presented. Although there is no guarantee that the minima recorded at the five stations during a given period occurred on the same night, the figures suggest a general gradient in minimum temperatures from the ridge top to the valley bottom. Minima at the lowest two stations are generally from 1 to 3°C less than those at the uppermost station (Table 6.7).

Another set of thermometers was stationed so as to cover the altitude range from 980m in the upper Broad River valley to 1300m on the summit of Mt. Mawson. This transect takes the form of a broad curve, extending across Wombat Moor and ascending the eastern slope of Mt. Mawson (Figure 6.4). This arrangement was chosen in preference to a straight transect from the Broad River Valley up the north-eastern slope of Mt. Mawson, because of the desirability of placing all thermometers in situations where the vegetation had a similar structure. The north-eastern slope of Mt. Mawson between about 1000 and 1220m carries open-forest to low open-forest (Table 7.2). A transect up this slope would have confounded the effect of increasing altitude with that of the presence or absence of the tree canopy. Six of the 11 thermometers on the altitudinal transect were located at the same six stations for which rainfall and evaporation data have been reported above. The remainder were interspersed between them. Maximum and minimum temperatures recorded over contiguous periods of about two weeks duration from 2 December 1981 to 16 April 1982 and for the 76 day period from 17 April 1982 to 30 June 1982 are presented in Table 6.8.

In general, minima do not show a systematic decline with increasing altitude. Indeed, the lowest minima often occurred at the lowest altitude station, in the upper Broad River valley, or at the

Observation Period		Temperature (°C)										
	Station Altitude (m)	1 980	1e 1050	2 1070	2a 1120	3 1150	3a 1190	4 1220	4a 1280	4b 1280	5 1280	6 1300
2/12/81 to 17/12/81 (15 days)	Minimum	-2.0	-1.5	-3.5	-2.5	-2.5	-1.0	-1.0	-1.5	-1.5	-1.0	-1.0
	Maximum	25.5	23.5	28.5	26.0	29.0	27.5	26.5	29.0	27.0	24.5	24.0
18/12/81 to 31/12/81 (14 days)	Minimum	-1.0	-2.5	-2.5	-2.5	-2.5	-2.0	0.0	-1.5	-1.0	-0.5	-1.0
	Maximum	29.5	29.0	31.0	28.5	28.5	29.0	27.5	29.5	27.5	25.0	23.5
1/ 1/82 to 13/ 1/82 (13 days)	Minimum	-3.0	-3.0	-3.5	-3.0	-1.5	-1.0	-1.0	-2.0	-1.5	-1.5	-1.0
	Maximum	37.0	35.0	38.0	35.0	37.0	35.5	33.5	35.0	33.5	31.5	28.5
14/ 1/82 to 29/ 1/82 (16 days)	Minimum	-3.0	-0.5	-1.5	-0.5	-1.0	-0.5	0.5	-0.5	-0.5	-0.5	-0.5
	Maximum	38.0	36.5	37.5	36.0	37.0	35.5	36.0	35.5	35.5	31.5	30.0
30/ 1/82 to 12/ 2/82 (14 days)	Minimum	-3.0	-3.5	-3.0	-3.5	-2.5	-1.0	1.0	0.0	-1.5	0.5	0.5
	Maximum	33.5	32.0	34.5	32.5	33.5	31.0	32.0	31.0	30.0	27.0	25.0
12/ 2/82 to 4/ 3/82 (21 days)	Minimum	-4.0	-3.0	-2.5	-3.0	-2.5	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5
	Maximum	38.0	37.5	39.5	36.0	37.0	36.0	34.5	35.5	33.5	32.0	30.0
5/ 3/82 to 17/ 3/82 (14 days)	Minimum	-1.0	0.0	-1.0	-0.5	-1.0	-1.0	-1.0	-1.5	-1.5	-1.0	-1.0
	Maximum	33.0	31.5	34.0	32.0	32.0	30.5	30.0	31.5	29.5	27.5	26.0
18/ 3/82 to 31/ 3/82 (15 days)	Minimum	-1.0	0.0	0.0	-1.0	0.0	-4.0	-1.5	-3.5	-5.0	-0.5	-1.0
	Maximum	28.0	27.5	30.0	26.5	29.0	28.0	26.0	27.0	25.0	23.5	21.0
1/ 4/82 to 16/ 4/82 (16 days)	Minimum	-3.5	-1.5	-2.0	-2.0	-2.0	-2.5	-2.5	-3.0	-2.5	-3.0	-2.0
	Maximum	27.5	26.0	28.5	25.0	27.0	26.0	24.0	26.5	24.0	22.5	20.5
17/ 4/82 to 30/ 6/82 (76 days)	Minimum	-11.0	-9.0	-9.0	-9.0	-8.5	-6.5	-5.5	-6.0	-7.0	-6.5	-6.5
	Maximum	21.0	19.5	22.5	19.5	21.0	19.5	18.0	18.5	16.5	14.5	13.5

Table 6.8 Minimum and maximum temperatures recorded along an altitudinal transect from the upper Broad River valley to Mt. Mawson. For locations of stations see Figure 6.4

stations on Wombat Moor, while the minima at the stations on Mt. Mawson were from 1 to 4°C higher. It therefore appears that inverted temperature gradients, due to cold air drainage, occur at a relatively large scale on the plateau top, as well as at the small scale observed in the upper Broad River valley. The observations show that frosts occurred at all stations throughout the 1981-1982 summer. The minima for the 76 day period from 17 April to 30 June show a systematic increase, from -11°C at station 1 in the upper Broad River valley to -6.5°C at station 6, near the summit of Mt. Mawson.

Maximum temperatures displayed considerably more variation than could be explained by even the most generous lapse rate over an altitude range of 420m. Maxima at station 6 were often between 7 and 9°C lower than those at station 1 (Table 6.8). It is likely that radiative heating of the thermometers occurred, despite attempts to shield them. The amount of foreground reflection may have been considerable at some stations. A significant fraction of the relative depression in maxima at stations 4b, 5 and 6 may have been due to convective cooling by the wind, since these three stations were the most wind-exposed. These obsevations illustrate some of the difficulties involved in obtaining ecologically meaningful temperature data.

6.5.6 Sunshine, Cloud and Humidity

Data for Maydena (Table 6.4) show that the mean number of hours of bright sunshine per day varies from 6.8 in January to 1.8 in June. Also presented in Table 6.4 are the mean numbers of clear days and cloudy (overcast) days observed during each month at Maydena. Clear days are most frequent in January and February. At least one clear day may be expected in each month from April to September. Cloudy days are most frequent from May to August and least frequent in January and February. The data for Maydena is broadly indicative of conditions on the Mt. Field Plateau. However, low-lying cloud or fog does not affect the plateau top. In addition, the elevated horizon at Maydena, due to surrounding mountains, probably reduces the amount of direct solar radiation. For both these reasons, it is likely that the number of hours of sunshine per day is somewhat greater at sites on the plateau top than at Maydena.

Mean relative humidity at Maydena, measured at 9 a.m., ranges from 92% in June and July to 70% in December (Table 6.4). Corresponding figures for 3 p.m. vary from 79% in June to 49% in January. Daily departures from these averages are considerable, especially in the summer months. When an intense anticyclone located to the east of Tasmania extends a ridge from over the Australian continent, the resulting north to north-westerly air stream causes an incursion of hot, dry air across the island. The relative humidity may then fall to less than 10%. If forest fuels are dry and the winds are strong, the chances are that any bushfires which occur will be widespread and devastating.

6.6 Disturbance

Disturbance of the vegetation on the Mt. Field Plateau by the activities of man has been primarily via his influence on the frequency of occurrence of destructive wild-fires. The vast majority of bushfires in Tasmania are of human origin (Jackson and Bowman 1982). Rare fires caused by lightning strikes are almost invariably extinguished rapidly by the associated rain. Although European man did not colonise Tasmania until the early nineteenth century, there is abundant evidence that aboriginal man has been present on the island since the late Pleistocene. Goede and Murray (1977) described stone implements and charcoal found in a limestone cave deposit in the Florentine Valley, immediately to the west of Mt. Field. Radiocarbon dates suggested human presence in the area prior to 12600 BP. The recent discovery of stone implements on glacial moraines in the Broad River Valley (K. Kiernan, personal communication 1983) indicates that aboriginal man has visited the Mt. Field Plateau since deglaciation.

The Tasmanian aboriginals regularly set fire to vegetation as part of their hunting and land management practices (Jones 1969). It is therefore probable that periodic wild-fires have occurred on the Mt. Field Plateau throughout the Holocene. Most of the subalpine forests and woodlands within the study area appear to have been burnt at least once during the past 150 years. However, specimens of Eucalyptus coccifera with stem diameters exceeding 100cm are sometimes found on boulderfields, which form a natural barrier to fire. Cores taken from some trees of this size suggested ages in excess of 200 years. However, in most situations the largest individuals of E. coccifera have stem

diameters of 20cm or less. The generally subdominant Symphyomyrtus species E. subcrenulata and E. urnigera often take the form of a group of suckers arising from a lignotuber. Dense, apparently even-aged, stands of woolly tea-tree (Leptospermum lanigerum), sometimes forming an understorey beneath eucalypt forest, may result from a pulse of regeneration following fire.

The most recent fires affecting the study area occurred in 1961 and 1966. The 1961 fire, mentioned in section 6.5.3, burnt out most of the Humboldt Valley. It extended onto the plateau top in several places along the south-western margin of Mawson Plateau and the southernmost fringe of Wombat Moor. In 1966 a "controlled" forestry burn in the Florentine Valley devastated the western slopes of the Mt. Field Plateau and most of the valley occupied by Lawrence Rivulet. Spot fires from this escape destroyed Athrotaxis cupressoides dwarf coniferous woodland on the eastern slope of the Rodway Range, south-west of James Tarn, and on the Tarn Shelf near Lake Newdegate. The effects of fire on alpine plant communities in Tasmania have been discussed by Kirkpatrick, Dickinson and Cantle (1982).

Human disturbance of the vegetation in the study area, other than that associated with fire, is restricted mainly to the vicinity of the Lake Dobson road and the ski developments on Mt. Mawson. Roads, tracks, cleared land and buildings collectively occupy less than one percent of the area. There has been some cutting of trees south of the road across Wombat Moor and in the vicinity of the huts around Lake Dobson, presumably for firewood or track cording, but the areas affected are of very limited extent.

In an attempt to extend the duration of snow cover and eliminate obstacles to skiers, some "slope grooming" has been performed near the ski tows on Mt. Mawson. The removal of the surface layer of boulders and the associated shrubberies has resulted in soil erosion. Attempts to stabilise the soil, using exotic grasses such as Poa pratensis and a straw mulch, have resulted in the introduction of agricultural weeds such as Taraxicum officinale, Leontodon leysseri and Cirsium vulgare. Exotic weeds, mostly composites, have also been observed along the sides of the Lake Dobson road and on those areas burnt in 1961 and 1966.

Lake Fenton forms part of the water supply system for Hobart. A gutter has been excavated along the slope to the west of Wombat Moor in order to re-direct runoff and ground water from the moor eastwards into Lake Fenton. The slope is covered with yellow-brown solifluction soils (see section 6.3) with an impermeable iron pan at a depth of about 30 to 45cm, which results in a perched water table. The gutters cut through this iron pan, thus interrupting the downslope flow of soil water. Towards the end of the relatively dry 1980-81 summer (rainfall at Lake Fenton in December to February was only 40% of average), the death of large numbers of individuals of Leptospermum lanigerum was observed in the dense, even-aged stand immediately downslope of the gutter. This was almost certainly the result of drought, since no death of the species occurred upslope of the gutter. Similar local effects on the vegetation downslope of the Lake Dobson road are probably attributable to the diversion of natural drainage patterns.

6.7 Previous Vegetation Studies

The vegetation of the Mt. Field Plateau has been described by Gibbs (1921), Schweinfurth (1962), Jackson (1974), Davies (1978), Macphail (1975, 1979) and Ogden and Powell (1979). The accounts of Gibbs (1921) and Schweinfurth (1962) both emphasise phytogeographical aspects, while the descriptive treatment of Macphail (1975, 1979) was intended to provide a background to palynological studies.

Jackson (1974) provided a list of plant communities occurring in the Mt. Field National Park, which covers most of the plateau. Primary subdivisions were based on community structure (height and cover of the dominant stratum) and altitude. Each structural/altitudinal type was further subdivided according to the floristics of the dominant stratum. In all, 147 community types were delineated. Davies (1978) classified the vegetation of the Mt. Field National Park into 43 community types using floristics, particulary of the dominant stratum, as the main criterion. The dominance-types were further subdivided by structure, using the system of Specht (1970), giving a total of 83 vegetation units. Davies (1978) considered that a considerable number of the communities listed by Jackson (1974) were "...not recognisable units of recurring vegetation". The dominant species of some of Jackson's communities were not recorded on the Mt. Field Plateau by Davies (1978) and have not been observed in the present study. This suggests that Jackson may have inferred the presence at Mt. Field of some communities observed on other Tasmanian dolerite plateaux, without direct field observations of their presence.

The classifications of both Jackson (1974) and Davies (1978) were derived after a consideration of extensive field observations, but without the use of rigorous sampling or formal analytical methods. Ogden and Powell (1979) described the altitudinal zonation of forest vegetation along the Lake Dobson road from the National Park township to Mt. Mawson, an altitudinal range of about 1060m. They used a plotless sampling technique, with the emphasis on trees and large shrubs, but also obtained lists of understorey species. The data were subjected to a direct gradient analysis, with respect to altitude, and also analysed using various ordination and numerical classification techniques. The results suggested three broad altitudinal zones separated by fairly well-marked discontinuities. Ogden and Powell (1979) also described altitudinal variation in the number of woody species. Some aspects of their study will be criticised later.

CHAPTER 7 : SAMPLING AND DESCRIPTION

7.1 Vegetation

The extensive quantitative sampling of the subalpine and alpine vegetation of the Mt. Field Plateau, which forms the basis of the present study, was limited to the region indicated in Figure 7.1. The study area covers an area of approximately 16km^2. It is bounded to the south-east by a steep escarpment, marking the edge of the eastern plateau surface. The south-western boundary is formed by the Rodway Range and the south-western margin of the Mawson Plateau, while the northerly and southerly limits were arbitrarily defined by east-west trending sampling traverses (see below). Elevations within the study area range from c.900m, in the upper reaches of the valley occupied by Lady Barron Creek and near the shores of Lake Seal, to c.1370m on the highest peaks of the Rodway Range. The region includes gently sloping areas such as Wombat Moor, Mawson Plateau and the Tarn Shelf and steep slopes. The head wall of the cirque occupied by Lake Seal rises 310m to Tarn Shelf in a horizontal distance of only 350m. The vegetation of the study area is believed to be representative of the entire plateau top above 900m, although some species known to occur on the peaks west of the Rodway Range (Davies 1978) were not observed within the study area.

Within the study area, the upper altitudinal limit of the Tasmanian snow gum (Eucalyptus coccifera) is c.1220m. Stunted individuals of mallee form are sometimes found up to c.1250m, in situations such as Tarn Shelf, which are topographically protected from the full force of west to south-westerly storms. For convenience, that part of the study area above the limit of E. coccifera will henceforth

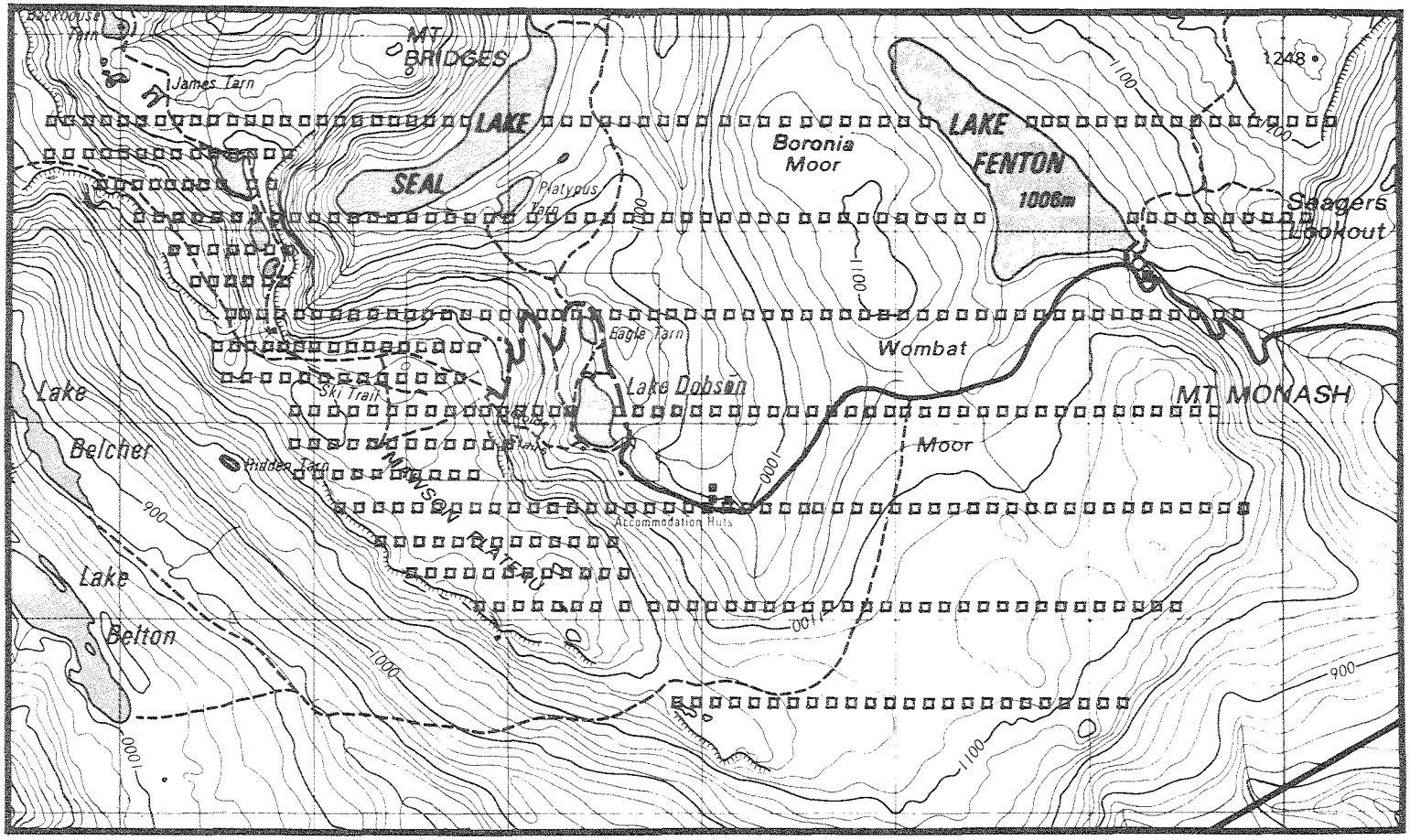


Figure 7.1 Map of the study area, showing the positions of the 438 vegetation sampling points (□). The map is reproduced from the 1:50000 scale sheet of Mt. Field National Park with the permission of the Lands Department.

be referred to as "alpine", and that below this limit will be designated "subalpine". Since E. coccifera does not generally form a clear-cut treeline, the boundary between these two tracts is somewhat arbitrary in places.

The major objective in sampling the vegetation was to obtain quantitative data representative of the full range of compositional variation occurring in the study area. Prior familiarity with the vegetation of the region, together with previous classifications (Jackson 1974; Davies 1978), suggested a complex pattern of potentially intergrading communities. In order to cover the entire range of variation, a large number of samples was required.

In designing the sampling scheme, statistical desirability had to be balanced against practical realities. The rugged nature of the terrain would have made the location of random sampling points extremely difficult and time-consuming. Totally random or stratified random sampling was therefore considered unfeasible. Instead, a randomly sited, systematic design was employed, with samples located at 100m intervals along traverse lines. Since most of the major topographic features in the study area have an approximately north-south trend, the sampling traverses were oriented east-west. Consequently, each line of samples crossed a range of topography. The traverse lines and sample locations were marked on stereo aerial photographs, with the position of the first sample on each traverse being chosen at random, close to the eastern boundary of the study area. The location of the starting points for each traverse on the ground proved relatively easy, with reference to prominent features on the photographs. Thereafter, the sampling traverse was surveyed with the help of frequent bearings from a

prismatic compass and periodic cues provided by the aerial photographs. The 100m interval between sampling points was estimated by pacing, with the "dead-reckoning" position being corrected, if necessary, by reference to features on the photographs.

Initially, seven traverses were surveyed. The southernmost was located about 500m north of the southern edge of the plateau and the traverses were spaced 500m apart. This gave a total of 325 samples, only 60 of which were located in the alpine zone. For the purpose of direct gradient analysis against altitude, it was deemed desirable to increase the number of alpine samples. Consequently, an additional two traverses were surveyed between each pair of existing traverses in the alpine zone. The spacing of the traverses in the alpine zone was thus reduced to 167m. This gave 173 alpine samples, and an overall total of 438. The locations of the samples are shown in Figure 7.1.

The choice of a suitable sampling unit was complicated by the fact that the vegetation encompasses a fairly wide range of structural types, with dominant growth forms varying from trees to low shrubs and graminoids. The sampling unit adopted was a $100m^2$ rectangular quadrat, measuring 20 X 5m. Quadrats of this area have been considered satisfactory for sampling alpine and subalpine vegetation in Tasmania by Kirkpatrick (1983). The quadrat was marked out using a length of nylon rope, with loops at the corners of the rectangle being secured by means of elasticised luggage hooks. The rectangular shape was chosen in preference to a square or circle for practical reasons: it was easier to lay out in dense scrub and forest and easier to search systematically than an isodiametric unit. Where species distributions are patchy or

clumped, the use of an elongated, rather than isodiametric sample may be advantageous in reducing sample to sample variation (Clapham 1932; Bormann 1953). While a sample area of $100m^2$ was thought suitable for most of the vegetation, reconnaissance surveys suggested that a smaller unit may be more appropriate for some of the alpine and tree-less subalpine communities. It was therefore decided to sample simultaneously at a smaller scale, by delimiting a sub-quadrat of $10m^2$ at one end of the $100m^2$ quadrat. Thus two sets of vegetation data, corresponding to the two scales of sampling, were collected concurrently. However, the data sets are not independent, since the vegetation occurring in the $10m^2$ sub-quadrat at each sampling site was a sub-set of that within the $100m^2$ quadrat.

At each sampling point, the 20 X 5m quadrat was established, taking care to ensure that it did not cross any apparent edaphic or topographic discontinuities and that the vegetation occurring within the quadrat was relatively homogeneous. Numerous attempts to quantify the assessment of homogeneity in vegetation (e.g. Dahl 1960) have met with limited success. It appears likely that absolute homogeneity, no matter how it is defined, is never attained in real vegetation (Goodall 1954b). In the present study, an area of vegetation was considered to be homogeneous if no consistent differences in flora, involving several species, appeared to occur between sub-areas within it. In several cases, heterogeneity did not become apparent until the quadrat had been laid out and recording was in progress. When this occurred, recording was completed but the sample was not included in any subsequent analyses. The total number of samples rejected because of heterogeneity was 14.

Having laid out the 20 X 5m quadrat a rectangular sub-quadrat of $10m^2$ was delimited at one end. With the exception of aquatic macrophytes in tarns and ponds, all vascular plant species with foliage occurring above the $10m^2$ quadrat were listed. An estimate of their projective canopy cover was recorded, using the six point scale shown in Table 7.1. This scale is modified from that used by Specht (1970), for the characterisation structural types in Australian vegetation. The use of cover classes, rather than precise measurements of cover, was a practical necessity, in view of the large number of samples to be collected and the limited time available. Nevertheless, it was felt that the system of classes employed would retain most of the relevant "information" concerning underlying environmental relationships. Subsequent analyses (see Chapter 9) tend to confirm this proposition. Species which could not be identified at the time of sampling were collected for later determination.

When the recording of vegetation data for the $10m^2$ sub-quadrat was complete, a list of the additional vascular species occurring in the remainder of the $100m^2$ quadrat was compiled. Cover estimates were then made for all species recorded over the $100m^2$ quadrat. Details of the structure of the vegetation, including the number of strata, the height and total projective canopy cover of the tallest stratum and the floristic composition of the dominant stratum (generally the tallest) were also noted. In addition to the vegetation data, observations were made of a number of site characteristics. These will be detailed in the following section.

Working without assistance, it proved possible to complete an

Cover Class	Projective Canopy Cover (%)	
	Class Limits	Class Midpoint
1	+ - 0.1	0.05
2	0.1 - 1	0.55
3	1 - 10	5.5
4	10 - 30	20.0
5	30 - 70	50.0
6	70 - 100	85.0

Table 7.1 The system of cover classes used in sampling the alpine and subalpine vegetation of the Mt. Field Plateau.

average of about six samples per day, although sampling time varied with the nature of the vegetation and the terrain. Interruptions by inclement weather were reasonably frequent, and on one occasion the recording of a sample was delayed by an aggressive tiger snake (Notechis ater humphreysi). In all, the collection of 438 samples required 77 complete days in the field.

7.2 Site Characteristics Measured or Estimated Directly

At each sampling point, several site characteristics considered to be indicative of environmental factors of operational significance to plant species were recorded. Because of practical limitations, recording was restricted to those features which could be rapidly determined. No attempt was made to measure soil properties (e.g. pH) or to collect soil samples for chemical and/or detailed textural analysis. Since the study area is geologically uniform, gross variation in the nutritional status of the soils was not expected (see section 6.4). The characteristics recorded included the slope angle, the aspect or azimuth rounded to the nearest octant (i.e. N,NE,E etc.), the proportion of the ground surface covered by dolerite boulders or exposed bedrock, topographic position, the type of soil and its approximate depth, the apparent degree of exposure to west to south-westerly storms (arbitrary, relative scale) and the degree of internal drainage of the substrate.

Substrate drainage was recorded using a system of five classes, closely related to the drainage catena recognised by Dimmock (1961). The criteria used to define these classes were as follows :

(1) Waterlogged - High Moor Peats with the water table at or near the ground surface, except in very dry spells during the summer

months. Waterlogged conditions are generally associated with level or gently sloping sites or shallow basins. Tarns and small ponds commonly occur on such sites.

(2) Poorly drained - High Moor Peats, with the peat layer commonly between 30 and 40cm in thickness in the subalpine zone. The water table is generally lower than in class (1). Poorly drained conditions are usually associated with gently sloping terrain.

(3) Intermediate - Yellow-brown soils on solifluction deposits or lithosols with shallow peat development. Where an iron pan has developed, there is often a perched water table at a depth of 30 to 45cm. Such conditions generally prevail on gentle to moderate slopes. In the subalpine tract, such slopes are sometimes fed with a more or less continuous supply of ground water from the moorland above.

(4) Well drained - Yellow-brown soils or rocky lithosols with no peat development. Well drained conditions generally occur on moderate to steep slopes, ridges or peaks.

(5) Excessive - Boulderfields and screes with minimal soil accumulation in the surface 30-100cm. In such sites, the boulders may extend to a depth of several metres. Sometimes, they are underlain by clay-loam or sandy clay-loam.

7.3 Derived Site Characteristics

The altitude of each sampling site was estimated to the nearest 10m, by cross-comparison between the stereo aerial photographs and the 1:50000 scale topographic map of the region produced by the Lands Department (1976). Although the contours on the map are form lines, produced with minimal ground control, the estimated altitudes are believed to be accurate to within 10m.

An estimate of the annual solar radiation at each site was obtained using the computer program CLOUDY. The program incorporates the model atmosphere approach described by Fleming (1971), for the calculation of clear-day solar radiation on any surface. Cloudiness is taken into account by using regional data on the mean number of hours of bright sunshine per day in each month and atmospheric precipitable moisture content is estimated using regional monthly data on mean humidity. Sunshine and humidity data for the Maydena station (section 6.5.6) were employed for these purposes.

For each sampling site, the altitude, slope angle and slope azimuth had been recorded in the field. For those situations in which direct radiation was likely to be reduced by high ground in the northern sector, additional data on the elevation of the real horizon at several compass bearings were determined. This information was digitised from the 1:50000 topographic map, using a program specially developed for an Hewlett-Packard model 9825A desktop computer system. In view of the quality of the data and the assumptions made in the program CLOUDY, the absolute precision of the derived estimates of mean annual solar

radiation is questionable. However, they do provide a useful measure of the relative variation between sites. The annual solar radiation estimates ranged from 16.5Kj/cm^2, for sites on steep, north-facing slopes to 9.1Kj/cm^2 on steep southerly slopes. The value for level sites with low real horizons was 15.1Kj/cm^2.

7.4 Nomenclature

Taxonomic nomenclature is based largely on Curtis (1963, 1967) and Curtis and Morris (1975) for gymnosperms and dicotyledons, Willis (1970) for monocotyledons and Jones and Clemesha (1981) for ferns and lycopsids. The authorities for the nomenclature of all species encountered during sampling of the vegetation are given in Appendix B.

The existence of genetic complexity, in the form of hybridisation between some pairs of con-generic species, has been observed within the study area. Cyathodes parvifolia intergrades extensively with C. juniperina in the vicinity of Lake Fenton and a range of morphological forms is generally present at a given site. No attempt was made to differentiate these two species in the present study, all plants being recorded as C. parvifolia. Intergradation between Cyathodes straminea and C. glauca was also apparent at some sites. However, the more obvious morphological differences involved in this case generally permitted the assignment of intermediate individuals to the species to which it bore the closest resemblance. Both C. juniperina and C. glauca reach their maximum development at Mt. Field on the slopes of the plateau, below 900m in altitude. C. parvifolia and C. straminea are largely confined to the plateau top.

Orchids were occasionally observed during vegetation sampling and those found in the samples were recorded. However, orchids were not included in any of the subsequent analyses, since their ephemeral nature makes their records fragmentary and unreliable. The species observed were Acianthus viridis Hook. f., Caladenia catenata var. minor (Hook.f.) W.M. Curtis, Prasophyllum alpinum R. Br. and Pterostylis alpina R.S. Rogers.

In naming structural types in the vegetation, a system modified from that proposed by Specht (1970) was used. The scheme, which is outlined in Table 7.2, is based on the growth-form, height and projective canopy cover of the tallest stratum. For the purpose of this scheme, a tree is defined as a woody plant, generally taller than 5m and with a single major stem, while a shrub is a woody plant generally shorter than 5m and with several stems arising near ground level. The dominants of the dwarf forest and woodland types were still regarded as trees, since they can exceed 5m in height in other situations on the plateau.

Growth-form and height of Tallest Stratum	Projective Canopy Cover of Tallest Stratum			
	70-100%	30-70%	10-30%	<10%
Trees 10-30 m	closed-forest	open-forest	woodland	-[1]
Trees 5-10 m	low closed-forest	low open-forest	low woodland	-[1]
Trees <5 m	dwarf closed-forest	dwarf open-forest	dwarf woodland	-[1]
Erect shrubs >1 m	closed-scrub	open-scrub	tall shrubland	tall open-shrubland
Erect shrubs <1 m	closed-heath	open-heath	low shrubland	low open-shrubland
Prostrate shrubs	prostrate closed-heath	prostrate open-heath	prostrate shrubland	-
Cushion-forming shrubs	cushion closed-heath	cushion open-heath	cushion shrubland	-
Hummock sedges 0-2 m	closed-hummock sedgeland	hummock sedgeland	-[1]	-[1]
Herbs (including	closed-herbland[2]	herbland[2]	-	-
perennial forbs,	closed-grassland	grassland	-	-
grasses, sedges,	closed-sedgeland	sedgeland	-	-
cord-rushes (Restionaceae),	closed-rushland	rushland	-	-
the lily *Astelia alpina*,	closed-lilyland	lilyland	-	-
the fern *Gleichenia alpina*	closed-fernland	fernland	-	-
and mosses).	closed-mossland	mossland	-	-

[1] These communities were characterised structurally by the next tallest stratum.

[2] Appropriate names depend on the nature of the dominant herb.

Table 7.2 Structural nomenclature used for the subalpine and alpine plant communities of the Mt. Field plateau. Modified from Specht (1970). Aquatic communities and saxicolous lichen/bryophyte communities are not included.

CHAPTER 8 : DIRECT GRADIENT ANALYSIS

8.1 Introduction

From the beginning of the serious scientific study of vegetation the traditional emphasis was on the classification of plant communities into non-overlapping, generally hierarchical systems of units (e.g. associations, alliances and formations). Among the various classificatory schools, there was almost universal agreement that the units recognised were "natural", resulting from the operation of well-defined processes inherent in the development and maintenance of plant communities (Whittaker 1962, 1978b). The basic unit in most classificatory systems, the association, was generally defined as a vegetation unit whose member stands were relatively uniform in habitat conditions and in the structure, physiognomy and floristic composition of the vegetation, at least with respect to certain species (e.g. dominants, character species), and more or less distinct in some or all of these respects from members of other associations (Tansley 1920; Nichols 1923; Du Rietz 1929; Braun-Blanquet 1932; Pavillard 1935). Species were generally thought to be distributed in terms of the associations, so that all of the species which characterised a particular association had distributional limits corresponding with those of the association. The organisation of species into associations was understood to be the result of their common response to habitat conditions and of interactions between species, leading to their mutual co-adaptation. The set of concepts underlying this traditional view of the nature of of vegetation was so universally accepted that it was not considered necessary to name it as a theory. Whittaker (1956) has

subsequently suggested the title "community-unit" theory.

An alternative view of the nature of plant communities was expressed by a number of authors, including Ramensky (1924), Gleason (1926, 1939), Lenoble (1926) and Fournier (1927). These authors regarded plant species as individualistic. Each responded in its own unique way to the array of abiotic and biotic factors constituting its environment, so that no two species had identical distributions. Plant communities were considered to be the result of the overlap of individualistic species distributions, with each stand being essentially an individual phenomenon. The compositional variation between stands of vegetation was regarded as potentially continuous, making the delimitation of units such as associations a fundamentally arbitrary process. This view of vegetation, with its basic concepts of species individuality and community continuity, has been termed the "individualistic hypothesis" (Whittaker 1956). Goodall (1963) has pointed out that there is no necessary logical connection between the conception of vegetation as a continuum and the assertion that species are distributed individualistically. Nevertheless, the two concepts are closely linked historically, since authors embracing one concept have invariably supported the other as well (McIntosh 1967).

The debate between supporters of the community-unit and individualistic views of vegetation (see Gleason 1926; Nichols 1929; Cain 1947; Whittaker 1951; Webb 1954; Major 1961; Daubenmire 1960, 1966; Goodall 1963; Cottam and McIntosh 1966; McIntosh 1967; Langford and Buell 1969) has been hampered by a lack of suitable data. Prior to about 1950, most sets of vegetation data were obtained using sampling procedures which assumed the existence of discrete associations. Hence

they can not be used in an objective test of the validity of the association concept. The need for suitable data led R.H. Whittaker to the development of a research approach which has subsequently been termed "gradient analysis" (Whittaker 1967). The approach is exemplified by numerous studies of Whittaker and his students (e.g. Whittaker 1956, 1960; Whittaker and Niering 1965; Westman 1975; Peet 1978, 1981). A related set of techniques was independently developed by the "Wiconsin School" of J.T. Curtis (Curtis and McIntosh 1951; Brown and Curtis 1952; Curtis 1955; Bray and Curtis 1957; Maycock and Curtis 1960). It is now recognised that similar approaches can be traced back to the work of the Russian geobotanist L.G. Ramensky during the 1920's and 30's (review by Sobolev and Utekhin 1978).

The objective of gradient analysis is an understanding of the manner in which the performance of individual species and the characteristics of communities change along major environmental gradients. Whittaker (1967) distinguished two complementary approaches within gradient analysis. "Direct gradient analysis" entails the arrangement of vegetation samples according to indices of position along recognised environmental gradients. The way in which the performances of species and the characteristics of communities vary along these gradients is then studied. In "indirect gradient analysis", vegetation samples are arranged into abstract compositional series, solely on the basis of data on the presence or abundance of species. Subsequently, the patterns of environmental variables within the resulting arrangements are examined, in order to elucidate relationships between the extracted compositional gradients and underlying environmental gradients.

The direct approach is the more fundamental, since the design of effective methods for indirect gradient analysis requires an understanding of the way species respond to environmental gradients. Provided that the major environmental gradients affecting the vegetation can be recognised in advance, and that suitable indices of the positions of samples along these gradients are available, direct gradient analysis can be a rewarding approach to the elucidation of vegetation-environment relationships. The approach is purely descriptive and the observed relationships between community characteristics, species performances and environmental gradients are correlative, rather than causal. However, experimental studies, aimed at elucidating the mechanisms underlying these relationships, require a solid observational foundation.

Evidence from direct gradient analysis is also required for the development of species niche theory (May 1974) and for the conceptual development of evolutionary ecology. Whittaker (1967) has interpreted the results of his direct gradient analyses as indicative of an evolutionary tendency for the degree of direct competition between species to be reduced, through the divergence of their modes along environmental gradients. Other authors (e.g. Mueller-Dombois and Ellenberg 1974; Goodall 1965) have suggested the opposite trend, leading to species with parallel or closely similar distributions.

A number of methodological problems in direct gradient analysis have been identified. Daubenmire (1966) stressed the need, when attempting to examine species distributions along a particular gradient, to stratify with respect to other recognised gradients. If this is not

done, the confounding of the effects of other gradients can lead to ambiguous or misleading results. Among recent applications of direct gradient analysis, the study of an altitudinal gradient in forest types at Mt. Field by Ogden and Powell (1979) confounds the effects of variation in geology, slope aspect and soil drainage with the primary gradient of altitude.

A more fundamental problem is that of the definition and quantification of environmental gradients. Austin and Cunningham (1981) have suggested the term "indirect environmental gradient" to refer to gradients such as altitude, where the variable used as an index of position has no direct effect on plant growth. The nature and strength of the relationships between the underlying, physiologically active variables and the variable defining an indirect environmental gradient may change with geographical location. Austin and Cunningham (1981) also distinguished "direct environmental gradients", defined by variables which have a direct physiological effect on plant growth (but are not resources for which exploitative competition may occur) and "resource gradients", defined by the availability to plants of some essential resource. They suggest that the failure to distinguish between these three different types of environmental gradients may have contributed to confusion in the debate over the form of species response curves.

It is often difficult to devise a suitable index of position along environmental gradients which is amenable to measurement. Difficulties in quantifying the "topographic moisture gradient" (from valley bottoms to exposed ridges) led Whittaker (1956, 1960) to the use of an indirect

approach, based on the assignment of moisture scores to species and the derivation of indices of site position along the moisture gradient using weighted averages. This approach is a form of indirect gradient analysis. The use of sample arrangements derived from species data in order to study species distributions involves an element of logical circularity which should be avoided (Whittaker 1967; Austin 1972). Other approaches to the quantification of environmental gradients are the use of scalars (Loucks 1962), which take account of the compensating effect of one abiotic factor on another, and the derivation of synthetic indices from readily measured variables using environmental process models. As an example of the latter approach, Austin (1971) derived a moisture stress index from rainfall, evaporation, solar radiation and estimates of the moisture storage capacity of the soil.

Another aspect of direct gradient analysis in which methodological improvements are required, is in the fitting of species response curves. The traditional approach has been to divide the gradient into segments, compute the mean abundance of a species in each segment and then to draw a free-hand curve through the average points. Often the points are smoothed before drawing curves, using a moving average technique (cf. Curtis and McIntosh 1951). The necessity for a statistical assessment of the adequacy of fit of response curves has been stressed by Austin and Cunningham (1981), who have experimented with the use of Generalised Linear Modelling (GLM) (Nelder and Wedderburn 1972) for this purpose (see also Austin, Cunningham and Good 1983).

This chapter deals with the application of direct gradient analysis to the alpine and subalpine vegetation of the Mt. Field Plateau.

8.2 Informal Direct Gradient Analysis

8.2.1 Introduction

Section 8.2 describes an "informal" direct gradient analysis of the subalpine and alpine vegetation of the Mt. Field Plateau. The simple approach developed by Whittaker (1967, 1978a) has been followed. In section 8.3, the application of Generalised Linear Modelling, as a more rigorous approach to direct gradient analysis, is examined.

Extensive field observations, both prior to and during the present study, suggested that much of the vegetational variation could be related to two major environmental gradients. The first is a complex-gradient (sensu Whittaker 1956), involving joint variation in many factors. These include average and extreme temperatures, the duration of snow cover, the degree of exposure to glazing storms and the amount of precipitation. Site altitude will be used as a convenient index of position along this gradient, which will henceforth be termed the "altitudinal gradient". The altitudinal gradient is an "indirect environmental gradient" in the terminology of Austin and Cunningham (1981), since altitude itself has no direct physiological effect on plant growth. It is probable that the physiologically active variables which vary with altitude are of varying significance to different plant species, but investigation of this question must await future experimental studies. Some preliminary observations of the variation in daily maximum and minimum temperatures and rainfall along the altitudinal gradient have been presented in sections 6.5.5 and 6.5.3, respectively.

The second major environmental complex-gradient is related to the degree of internal drainage of the substrate. Drainage conditions vary from sites where the soil is almost permanently waterlogged and a layer of acid peat has accumulated, through moderately drained sites with shallow peat or a highly organic surface horizon, to sites with well drained, rocky soils and finally boulderfields and screes with minimal soil accumulation at the surface. The soil catena associated with the drainage gradient has been described in section 6.4. The system of five classes, described in section 7.2, was used to provide a crude index of site position along the drainage gradient. Like the altitudinal gradient, the drainage gradient is an "indirect environmental gradient" (sensu Austin and Cunningham 1981). A number of physiologically active variables would be expected to vary along this gradient. These include the reliability of soil moisture supply in summer, the degree of root aeration and pH. It is possible that these physiologically active factors are of varying importance in different segments of the gradient. At the waterlogged extreme of the gradient (class 1), poor root aeration and pH related effects may be of prime importance, while at the excessively drained end (class 5), soil moisture storage capacity may be a major limiting factor. Variation in the identity and relative importance of the physiologically active factors between different segments of a single complex-gradient may be a common phenomenon in nature (cf. van der Maarel 1980).

The following analysis examines the relationships between both the mean percentage cover of individual species and the values of various community characteristics (e.g. total cover, alpha diversity) and the environmental plane, or "ecoplane", defined by the altitudinal and

drainage gradients. In addition, the between-habit or beta diversity of the gradients is examined. The results of this analysis were taken into account when designing the vegetation-gradient models used in Part 1 of this thesis.

8.2.2 Methods

The analysis was based on the percentage cover data for the vascular plant species recorded in 438, 100m^2 rectangular quadrats (excluding orchids and aquatic macrophytes). The collection of this data has been described in section 7.1. From the full set of 438 quadrats, 14 were rejected because of heterogeneity in drainage conditions. A further 20 quadrats, which had been burnt during the 1960's (section 6.6), were also deleted. This was done to avoid confounding the effects of recent burning with those of the altitudinal and drainage gradients. Similarly, seven quadrats with very low annual solar radiation estimates (less than 11 kJ/cm^2) were excluded. This left a total of 397 quadrats for analysis.

The altitudinal range covered by the quadrats (910-1370m) was divided into nine classes, each 50m in width. Several quadrats with altitudes between 1360 and 1370m were nevertheless allocated to altitude class 9. The altitude classes were used in combination with the five drainage classes, to set up a two-way classification of the quadrats. The numbers of quadrats occurring in each of the 45 cells of the altitude X drainage classification are given in Table 8.1. Some combinations of altitude and drainage are represented by more than 20 quadrats, while a few cells are virtually unoccupied. The quadrats were distributed systematically, with the sampling intensity in the alpine

Altitude Class No.	Limits (m)	Substrate Drainage Class 1 Water-logged	2 Poorly Drained	3 Moderately Drained	4 Well Drained	5 Excessively Drained
9	1311-1360[1]	0[2]	1[2]	5	3	10
8	1261-1310	7	1	23	14	9
7	1211-1260	9	4	20	15	13
6	1161-1210	1[2]	5	18	3	17
5	1111-1160	10	6	11	7	23
4	1061-1110	11	8	21	6	18
3	1011-1060	5	5	24	3	10
2	961-1010	10	4	10	1	5
1	910- 960	0[2]	4	11	3	3

[1] Several sites with altitudes up to 1370 m were nevertheless allocated to altitude class 9.

[2] Combinations of altitude and drainage which are poorly represented in the study area.

Table 8.1 Numbers of samples occurring within each cell of the altitude by drainage classification used for direct gradient analysis.

zone (above c.1220m) being three times higher than in the subalpine zone (see section 7.1). If Table 8.1 is divided horizontally between altitude classes 6 and 7, the lower and upper sub-tables roughly correspond to the subalpine and alpine zones respectively. Within each sub-table, the relative numbers of quadrats occurring in each cell reflects the proportional representation, on an areal basis, of the various combinations of altitude and drainage in the alpine and subalpine landscapes.

Those cells with particularly low numbers of quadrats generally represent combinations of altitude and drainage which are uncommon within the study area. Poorly drained or waterlogged sites are rarely encountered above 1310m. Most of the terrain above this altitude consists of steep slopes and rocky peaks or ridges. Level areas occur at altitudes above 1310m on the western side of the Mt. Field massif. However, these were not sampled, due to the difficulty of access and time limitations. Waterlogged sites are also rare at altitudes between 1160 and 1210m within the study area. Most of the terrain at these altitudes consists of steep slopes, connecting the lower, eastern plateau surface with the higher surfaces (e.g. Mawson Plateau and the Tarn Shelf). The lack of waterlogged sites in the lowest altitude class also reflects the poor representation of this environmental combination in the landscape of the study area. The four cells corresponding to these poorly represented combinations of altitude and drainage have been left blank on the contour diagrams to be presented below.

Within each of the 41 occupied cells, mean values were computed for the percentage cover of individual species and for various community

characteristics. In computing the cover means for species, the integer cover class scores were replaced by the midpoints of the cover classes (Table 7.1). Only those 111 species for which the available data were considered adequate were included in the analysis. The community characteristics studied were:

(1) Total cover - the sum of the midpoint percentage cover values for all species occurring in a quadrat. This may be regarded as a crude index of standing crop.

(2) The height of the tallest stratum.

(3) Percentage dominance - the sum of the two highest percentage cover values in a quadrat, expressed as a percentage of total cover. This is a measure of the degree to which cover is concentrated into a few dominant species.

(4) Simpson's index, which is calculated as $\Sigma\ (Ci/T)^2$, where Ci is the percentage cover of the ith species in a sample, T is the total cover in the sample and the summation extends over all species occurring in the sample. This index, like percentage dominance, is a measure of the concentration of cover into a few dominants.

(5) Alpha diversity - the number of plant species per $100m^2$ sample. This was computed for the entire vascular flora, and for fractions of the flora represented by different growth-forms. The system of growth-forms employed is given in Table 8.2. The allocation of species to these categories is indicated in Appendix B. Alpha diversity was also partitioned simply into woody and non-woody components.

The minimum number of quadrats per cell considered to be acceptable for the computation of cell means was three. Values for the

Growth-form Category	Defining Comments (if necessary)	Number of Species	Percentage of Total
A. WOODY PLANTS			
Trees	Generally single-stemmed and reaching at least 3 m in height.	17	8.5
Erect or ascending shrubs	With many stems arising near ground level; less than 3 m high.	59	29.5
Climbing or twining shrubs	-	2	1.0
Prostrate or mat-forming shrubs	-	6	3.0
Cushion-forming shrubs	Peculiar "cushion" or "bolster" growth-form, with the apices of many short branchlets closely appressed, forming a compact surface.	3	1.5
		87	43.5
B. NON-WOODY PLANTS			
Graminoids	Monocotyledons with grass-like leaves or photosynthetic stems and scale leaves.	44	22.0
Perennial herbs	Dicotyledonous herbs, the above-ground parts persisting over winter.	53	26.5
Annual herbs and Geophytes	Dicotyledonous herbs, over-wintering as seeds or underground organs.	4	2.0
Ferns and Lycopsids	-	12	6.0
		113	56.5

Table 8.2 A classification, according to growth-form, of the vascular plant species encountered during sampling of the alpine and subalpine vegetation of the Mt. Field Plateau (excluding orchids and aquatic macrophytes).

two cells with less than three quadrats were obtained by weighted linear interpolation from the mean values for neighbouring cells. The interpolated mean cover value, M(i,j), for a cell representing altitude class i and drainage class j, was computed as:

$$M(i,j) = \frac{T(i+1,j) + T(i-1,j) + T(i,j+1) + T(i,j-1)}{n(i+1,j) + n(i-1,j) + n(i,j+1) + n(i,j-1)} \qquad (12)$$

where T(i,j) is the total of the percentage cover values for the species in each of the quadrats in the i,jth cell and n(i,j) is the number of quadrats in the i,jth cell. In the case of the (8,2) cell, the first terms in both the numerator and the denominator of this expression were ommitted, since the (9,2) cell was unoccupied.

Contours were fitted to the grids of mean cover values, using the computer program SURFACE II (Sampson 1978). The use of a computer routine for a similar purpose has been previously reported by Peet (1978). It avoids the subjectivity associated with the traditional practice of drawing contours by hand (e.g. Whittaker 1956). Contours were fitted to both the original grids of mean values, and after smoothing by a weighted moving average procedure. The smoothed value, M'(i,j), for the cell corresponding to altitude class i and drainage class j, was computed as:

$$M'(i,j) = \frac{F.T(i,j) + T(i+1,j) + T(i-1,j) + T(i,j+1) + T(i,j-1)}{F.n(i,j) + n(i+1,j) + n(i-1,j) + n(i,j+1) + n(i,j-1)} \qquad (13)$$

where T and n have the same meanings as in equation (12). The factor F is set equal to the number of neighbouring cells which contribute to the smoothing of the i,jth cell. For cells located in the body of the grid,

F=4. However, cells at the edges and corners of the grid have less than four neighbours. In such cases, the terms in the numerator and denominator of equation (13) which correspond to the missing neighbours, are omitted, and the value of F is reduced accordingly.

This form of smoothing takes account of the variation in the numbers of samples between cells. It was considered advantageous for species cover, since it tended to even out irregularities caused by occasional high cover scores in individual quadrats. However, the contour diagrams for community characteristics were not altered significantly by smoothing. In the case of species cover, special rules had to be devised to overcome some problems caused by zero values, which occur when a species is absent from all quadrats in a cell. The following conventions were adopted:

(1) Zero values were only smoothed if all the neighbouring values were non-zero. This rule prevented the artificial extension of species' ranges.

(2) In smoothing a non-zero value, neighbouring zero values were not permitted to contribute to the smoothing process. The terms in equation (13) corresponding to zero neighbours were omitted and the factor F was reduced accordingly. Without this convention, smoothing tended to cause a marked reduction of mean cover in all cells bordering a region where the species was absent.

(3) Non-zero values with at least one zero neighbour were not smoothed if all their non-zero neighbours were either greater than or less than the value to be smoothed. This rule was introduced to compensate for some undesirable consequences of rule (2).

The approach used in the present study to estimate the beta

diversities of the altitudinal and drainage gradients was similar to that of Peet (1978). The altitude X drainage classification described above was modified for the computation of beta diversities, by fusing adjacent pairs of the first eight altitude classes. This reduced the number of altitude classes to five and ensured a more adequate number of quadrats in the most sparsely occupied regions of the ecoplane. Nevertheless, the cells representing drainage classes 1 and 2 in the highest altitude class remained unoccupied. Within each of the 23 occupied cells, a composite sample was formed, by computing the mean percentage cover of all species in the quadrats falling into that cell. The compositional similarities of adjacent composite samples were then assessed. Both the percentage similarity coefficient (PS) and its binary equivalent, the Sorenson coefficient of community (CC), were employed for this purpose. The former is sensitive to changes in the mean cover of species along the gradients, while the latter reflects only floristic changes. The similarities, S, were converted into a measure of the amount of compositional change between adjacent composite quadrats, D, using the formula D=(100-S)/50. The D values between all pairs of adjacent cells along each of the five altitudinal and five drainage gradients were then summed, to obtain an estimate of the beta diversity of each gradient in half-change units. Peet (1978) attempted to correct for sampling errors, by subtracting the smallest D value from the D values for all pairs of adjacent composite samples. This procedure is unsound theoretically, since a pair of adjacent segments along a gradient can not be considered replicates in the normal statistical sense. They are known to differ in underlying habitat conditions, hence compositional differences between them cannot be

attributed entirely to sampling errors. No correction for "replicate similarity" was attempted in the present study.

Beta diversity values were also computed using the data for woody and non-woody fractions of the flora. This was done to investigate the possibility that beta diversities along the altitudinal and drainage gradients may vary independently between growth-forms.

8.2.3 Results and Discussion

8.2.3.1 Species Response Surfaces

Contour diagrams illustrating the smoothed ecological response surfaces (mean percentage cover) for 54 selected species are given as Appendix C. The species have been arranged in growth-form groups, largely according to the system outlined in Table 8.2. Inspection of these diagrams suggests that species are not organised into groups with similar distributions in relation to the altitude drainage ecoplane. The response surfaces display considerable variation in shape, although most appear to be unimodal. The locations of species modes appear to be scattered throughout the ecoplane. However, the coarseness of the grid, especially in relation to drainage, has limited the precision with which the modes and limits of the surfaces could be located in this analysis.

Examples of species whose response surfaces appear to be bell-shaped and symmetrical are Leptospermum lanigerum, Bauera rubioides, Richea sprengelioides, Exocarpos humifusus and Celmisia saxifraga. Species whose response surfaces are unimodal, but skewed, include Boronia citriodora, Diselma archeri and Poa gunnii. Microstrobos niphophilus and Telopea truncata have "shouldered" response surfaces. Many species reach their maximum mean cover at the edge of

the ecoplane. For species with such "truncated" distributions, it is usually possible to define the shape of the section through the response surface along its line of intersection with the edge of the ecoplane. The truncated surfaces of species such as Baeckea gunniana, Helichrysum backhousii and Gleichenia alpina are symmetrical, while those of Cyathodes straminea and Carpha alpina are skewed. The truncated surface for Eucalyptus coccifera has a "shoulder" along the edge of the environmental space defined by drainage class 5.

Several species have response surfaces which appear to possess more than one mode. Examples of such species are Leptospermum rupestre, Richea scoparia, Astelia alpina and Empodisma minus. For some species, some of the apparent modes are questionable, because of the considerable scatter of cover values around the means in most cells and the small numbers of quadrats in some cells. For example, the mode for Leptospermum rupestre at an altitude of c.1035m and drainage class 4, corresponds to a cell with only three quadrats.

Astelia alpina has one mode on moderately drained sites at altitudes greater than 1310m, and another on poorly drained to waterlogged sites at an altitude of c.1085-1135m. Mean cover declines as one moves away from either mode towards better drainage and/or lower altitudes. Empodisma minus has a broad mode on waterlogged to moderately drained sites at altitudes of 900-1100m and another on waterlogged sites at an altitude of c.1285m. The latter mode corresponds to a diminutive form which may prove to be genetically distinct. Richea scoparia appears to have three modes. One is centred on moderately drained sites at c.935m, where R. scoparia occurs in the

understorey of Eucalyptus subcrenulata open-forest, as an erect shrub up to 2m in height. The other two modes correspond to poorly drained sites at an altitude of c.1135m and waterlogged sites at an altitude of c.1285m. The structural form of the communities under both of these environmental combinations is generally open-heath. In such situations, R. scoparia is a compact shrub, generally less than 1m in height. The form occurring at these two modes has shorter, less recurved leaves than the lower altitude forest form. It is not known whether these morphological differences are the result of plasticity or genetic differentiation within the species. Menadue and Crowden (1983) have described a gradation in leaf morphology and flavenoid chemistry in R. scoparia, extending across Tasmania from the south-western to the north-eastern mountains. Most of the range of leaf morphology along this geographical gradient appears to be encompassed by the variation between populations along the altitude and drainage gradients at Mt. Field.

A more comprehensive examination of the forms of the ecological response surfaces for individual species was performed, using those 111 species for which sufficient data were available. These included the 54 illustrated in Appendix C. Response surfaces were classified visually as unimodal (possessing a single major peak) or complex (possessing more than one peak). The unimodal forms were further sub-divided into symmetrical (bell-shaped), shouldered, skewed and monotonic types. The latter category was introduced for species which attained their greatest mean cover at an edge or corner of the altitude X drainage ecoplane, and for which a section though the response surface where it intersected the edge of the ecoplane appeared to be more or less flat. The results of

	Unimodal				
	Symmetrical	Shouldered	Skewed	Monotonic (truncated)	Complex (Bimodal or Multimodal)
Trees	5 (50%)	1 (10%)	3 (30%)	1 (10%)	0 (0%)
Shrubs	24 (48%)	6 (12%)	8 (16%)	2 (4%)	10 (20%)
Woody Species	29 (48%)	7 (12%)	11 (18%)	3 (5%)	10 (17%)
Graminoids	10 (48%)	0 (0%)	5 (24%)	1 (5%)	5 (24%)
Herbs and Ferns	11 (37%)	1 (3%)	9 (30%)	2 (7%)	7 (23%)
Non-woody Species	21 (41%)	1 (2%)	14 (27%)	3 (6%)	12 (24%)
All Species	50 (45%)	8 (7%)	25 (23%)	6 (5%)	22 (20%)

Table 8.3 Visual classification, according to shape, of the response surfaces (mean percentage cover) of 111 species to the environmental plane defined by the altitude and drainage gradients. The entries in the table are the numbers of species whose response surfaces were of the indicated form. Figures in parentheses are percentages of the total number of species in the growth-form category represented by the corresponding row of the table.

the analysis are given in Table 8.3. Although 89 (80%) of the response surfaces were classified as unimodal, only 50 (45%) were bell-shaped and symmetrical. Complex response surfaces were exhibited by 22 (20%) of the species. When the full set of species was divided into woody and non-woody species, some differences in the proportional representation of response surface shapes became apparent. For example, complex response surfaces appear to be more common among non-woody species. In contrast, symmetrical, unimodal types are more frequent among woody species. The division of non-woody species into graminoids and non-graminoids, shows that the lower frequency of symmetrical unimodal response surfaces for non-woody species is due mainly to non-graminoids (Table 8.3).

Austin (1976a) presented the results of a visual classification of the shapes of 135 response curves along single environmental gradients. These were collated from five published gradient analyses. Only 24.5% of the curves were symmetrical and unimodal. 48.1% were unimodal, but skewed, and 27.44% were bimodal. As Austin pointed out, these results are probably biased, since the curves chosen for publication may have been selected to include a disproportionally large number of the more "interesting" asymmetrical or multimodal forms. The figures derived from two studies by Whittaker (1956, 1960) refer to the shape of response curves along altitudinal and topographic moisture gradients. These represent sections through the response surfaces to the ecoplane defined by the two gradients. When the abundance of a species is known to change systematically along more than one gradient, it is preferable to describe the shape of the response surface or hypersurface as a whole rather than one or more sections through the surface. If the latter

approach is used, confusing and ambiguous results may be obtained. For example, consider a species whose response surface with respect to gradients A and B is unimodal, but skewed in a direction parallel to gradient A. Sections through the response surface parallel to gradient A will appear skewed, while sections parallel to gradient B will be symmetrical.

The present results indicate that unimodal symmetrical response surfaces are not as uncommon as suggested by Austin's (1976a) analysis. Nevertheless, more than 50% of the species had surfaces which are either asymmetrical or multimodal. These results do not support the assertions of Gauch and Whittaker (1972a, 1976) and Westman (1980) that the majority of response curves (surfaces) are Gaussian. A recent analysis of species response curves along a soil nutrient gradient (Werger, Louppen and Eppink 1983) found that only 31% of species had responses which could be adequately fitted by a Gaussian curve.

For those 89 species whose response surfaces appeared to be unimodal, the position of the mode on the ecoplane and the mean percentage cover at the mode were estimated. The determination of modal positions was limited to the identification of the cell in the altitude X drainage classification in which the species attained its maximum mean cover. The mean cover (without smoothing) in that cell was taken as an estimate of the height of the response surface at the mode. The number of species whose modes occurred in each of the 41 occupied cells of the altitude by drainage grid is shown in Table 8.4. The modes are scattered throughout the two-way table, although their distribution is uneven. The frequency distribution of the number of modes per cell is given in Table 8.5. The mean number of modes per cell was 2.17, with a

Altitude Class No.	Limits (m)	Substrate Drainage Class 1 Water-logged	2 Poorly Drained	3 Moderately Drained	4 Well Drained	5 Excessively Drained
9	1311-1360[1]	-[2]	-[2]	2	3	2
8	1261-1310	4	2	0	0	0
7	1211-1260	5	2	0	3	2
6	1161-1210	-[2]	4	0	2	3
5	1111-1160	5	1	1	2	3
4	1061-1110	4	0	1	1	2
3	1011-1060	1	0	3	4	5
2	961-1010	3	1	2	1	5
1	910- 960	-[2]	4	1	2	3

[1] Several sites with altitudes up to 1370 m were nevertheless allocated to altitude class 9.

[2] Combinations of altitude and drainage which are poorly represented in the study area.

Table 8.4 Distribution of response surface modes for 89 species on the altitude by drainage classification used for direct gradient analysis. The entries in the table are the number of species whose modes occurred in the specified cell. Only those species whose response surfaces appeared to be unimodal were included.

All Species

No. of Modes per Cell	Observed Frequency	Expected Frequency
0	7	4.68
1	8	10.15
2	10	11.02
3	7	7.97
4	5	4.33
>5	4	2.85

$\bar{x}$ = 2.171

s^2 = 2.445

Goodness of fit test:

χ^2 = 2.39, d.f. = 4, p = 0.66

"Major" Species (Mean Cover at Mode >20%)

No. of Modes per Cell	Observed Frequency	Expected Frequency
0	32	31.35
1	7	8.41
>2	2	1.24

$\bar{x}$ = 0.268

s^2 = 0.301

Goodness of fit test:

χ^2 = 0.72, d.f. = 1, p = 0.40

Trees

No. of Modes per Cell	Observed Frequency	Expected Frequency
0	33	32.13
1	6	7.84
>2	2	1.03

$\bar{x}$ = 0.244

s^2 = 0.289

Goodness of fit test:

χ^2 = 1.37, d.f. = 1, p = 0.24

Shrubs

No. of Modes per Cell	Observed Frequency	Expected Frequency
0	14	15.46
1	16	15.08
2	9	7.36
>3	2	3.10

$\bar{x}$ = 0.976

s^2 = 0.774

Goodness of fit test:

χ^2 = 0.95, d.f. = 2, p = 0.62

Graminoids

No. of Modes per Cell	Observed Frequency	Expected Frequency
0	29	27.75
1	8	10.83
>2	4	2.42

$\bar{x}$ = 0.390

s^2 = 0.444

Goodness of fit test:

χ^2 = 1.83, d.f. = 1, p = 0.18

Other Non-woody Species

No. of Modes per Cell	Observed Frequency	Expected Frequency
0	26	23.40
1	8	13.13
2	6	3.68
>3	1	0.79

$\bar{x}$ = 0.561

s^2 = 0.702

Goodness of fit test:

χ^2 = 3.73, d.f. = 2, p = 0.15

Table 8.5 Tests of the hypothesis that species modes are randomly distributed over the environmental plane defined by the altitude and drainage gradients. In each case the observed frequency distribution of the number of species modes per cell is compared with the corresponding frequency distribution based on Poissonian expectation using a Chi-squared goodness-of-fit test.

variance of 2.45.

If the modes of species are distributed at random over the ecoplane, the frequency distribution of the number of modes per cell should be Poissonian. This expectation assumes that the size of the cells is such that the observed mean number of modes per cell is considerably less than the maximum number of modes which could potentially occur in a single cell (cf. Greig-Smith 1964). This approach to the assessment of randomness assumes that the spatial distribution of samples is random. In the present case, the samples (i.e. cells) form a contiguous grid, effectively covering the entire universe of interest. Hence the usual significance tests for the fit of the observed frequency distribution to that based on Poisson expectation may not be accurate. Nevertheless, a Chi-squared goodness-of-fit test was performed. The practice of combining classes whose expected frequencies are less than five was not followed, hence the test results should be conservative. The results of the test (Table 8.5) suggest close agreement with Poisson expectation (χ^2=2.39, d.f.=4, p=0.66). Thus species modes appear to be randomly distributed, at least at the scale represented by the altitude X drainage cells employed as samples.

The full set of 89 unimodal species was divided into four sub-sets, according to growth-form, and a similar test for a random distribution of modes was performed for each sub-set. The categories used were trees, shrubs, graminoids and other non-woody species. The results (Table 8.5) suggest that the modes of species within each growth-form category are randomly distributed over the altitude X drainage ecoplane.

Gauch and Whittaker (1972a, 1976) and Whittaker (1978a) have asserted that species modes are generally randomly distributed along environmental gradients. The present analysis supports this proposition. Gauch and Whittaker (1972a) also noted that the modes of "major" species (i.e. those with high modal abundances) sometimes tended to be more uniformly distributed along gradients. They interpreted this phenomenon as an expression of the "competitive exclusion" principle: the result of an evolutionary tendency for species modes to diverge along gradients, thus reducing the degree of direct competition between them. In the present study "major" species were arbitrarily defined as those unimodal species whose mean cover at the mode was at least 20%. There were 11 species which fulfilled this requirement. The number of major species modes occurring in each cell of the altitude by drainage grid was determined, and the frequency distribution of these counts was compared with that based on Poisson expectation, as described above. The results (Table 8.5) give no reason to suspect that the distribution of the modes of major species is non-random.

For those 89 species with apparently unimodal response surfaces, the frequency distribution of mean cover at the mode was tabulated (Table 8.6), using logarithmic class limits. The observed frequencies were compared with the frequencies expected for a lograndom distribution (i.e. equal frequency in each logarithmic class), using a Chi-squared goodness-of-fit test. The test indicated reasonable agreement (χ^2=21.27, d.f.=13, p=0.068).

The full set of 89 species was divided into woody and non-woody sub-sets, and the frequency distribution of modal mean cover was

Natural Logarithm of Percentage Cover at Mode Class Limits	All Species		Non-woody Species		Woody Species		
	Observed Frequency	Expected Frequency (Lograndom)	Observed Frequency	Expected Frequency (Lograndom)	Observed Frequency	Expected Frequency (Lograndom)	Expected Frequency (Lognormal)
<-2.5	2	6.36	2	2.79	0	3.57	0.07
-2.5 to -2.0	7	"	6	"	1	"	0.15
-2.0 to -1.5	6	"	5	"	1	"	0.36
-1.5 to -1.0	3	"	2	"	1	"	0.76
-1.0 to -0.5	6	"	4	"	2	"	1.51
-0.5 to 0.0	6	"	5	"	1	"	2.53
0.0 to 0.5	6	"	3	"	3	"	3.96
0.5 to 1.0	6	"	2	"	4	"	5.23
1.0 to 1.5	5	"	1	"	4	"	6.48
1.5 to 2.0	8	"	2	"	6	"	6.75
2.0 to 2.5	7	"	1	"	6	"	6.61
2.5 to 3.0	16	"	4	"	12	"	5.44
3.0 to 3.5	7	"	1	"	6	"	4.22
>3.5	4	"	1	"	3	"	5.95
		χ^2=21.27,d.f.=13 p=0.068		χ^2=13.77,d.f.=13 p=0.39		χ^2=36.80,d.f.=13 p=0.00045	χ^2=18.92,d.f.=12 p=0.090

Table 8.6 Frequency distributions of response surface height (i.e. mean percentage cover at the mode) for those species with apparently unimodal response surfaces. A logarithmic scale is used for response curve heights. Distributions are tabulated for both the full set of 89 unimodal species and sub-sets comprising woody and non-woody species. In each case the observed frequency distribution is compared with expectation based on a lograndom hypothesis (i.e. equal frequency in each logarithmic class) using a χ^2 goodness-of-fit test. The distribution for woody species is also tested for fit with a lognormal distribution.

examined for each sub-set (Table 8.6). For non-woody species, the observed frequency distribution was consistent with lograndom expectation (χ^2=13.77, d.f.=13, p=0.39), however the frequency distribution for woody species appeared to be widely divergent from a lograndom form (χ^2=36.80, d.f.=13, p=0.00045). Accordingly, the frequency distribution for woody species was tested for fit with a lognormal distribution (Table 8.6). The Chi-squared test suggested reasonable agreement (χ^2=18.92, d.f.=12, p=0.09). However, a plot of the observed and expected frequency polygons showed that the observed distribution was skewed to the right, relative to the fitted lognormal distribution and had a sharp peak. This peak is due to a particularly large number of woody species (mostly shrubs) with modal mean covers in the range 12 to 20%.

Gauch and Whittaker (1972a) suggested that the modal abundances of forest tree species along environmental gradients generally have a lograndom distribution. They also observed that modal abundances for forest herbs or of shrubs and herbs in desert coenoclines often follow a lognormal distribution. The present results provide some support for the concept of a lograndom distribution of modal abundances when all species are considered simultaneously. However, the results may be biased by the necessary exclusion of species for which there was insufficient data. For woody species, there is evidence that the frequency distribution of modal abundances does not agree with lograndom or lognormal hypotheses. This distribution is less likely to be biased than that for all species, since there were relatively few woody species without adequate data for construction of a response surface. Of the 89 species for which a response surface could not be defined, only 25 were

woody and 20 of these were of very localised and/or sporadic occurrence within the study area.

In addition to the the general shape of response surfaces, and the position and height of their modes, two other parameters of species response surfaces are of interest. These are the dispersions or ranges of occurrence of species along each of the two gradients. Gauch and Whittaker (1972a) stated that species dispersions along gradients are generally normally distributed, with a standard deviation equal to about 0.3 times the mean value. The results of the current direct gradient analysis were not suitable for a detailed investigation of this question. The investigation of the frequency distribution of ranges of occurrence should ideally be based on species whose distributions do not reach the end of any of the gradients studied. The altitude and drainage gradients on the Mt. Field Plateau do not have sufficiently high beta diversities (see section 8.2.3.4) for significant numbers of species to display distributions free from truncation at one or both ends of either gradient. A further inadequacy of the present data for the study of distributional ranges is the relatively coarse segmentation of the gradients, especially the drainage gradient. This would severely limit the precision with which the ranges of species along the gradients could be determined.

8.2.3.2 Trends in Community Characteristics

The contour plot for the mean height of the tallest stratum (Figure 8.1) shows that this aspect of community structure is closely related to the altitude X drainage ecoplane. Mean height reaches a maximum of more than 14m on well drained sites and boulderfields at altitudes less than 1000m. Such sites carry open-forest or woodland dominated by Eucalyptus coccifera. With increasing altitude and/or deterioration in drainage conditions, the mean height of the tallest stratum decreases. Under moderately drained to excessively drained conditions, the stature of E. coccifera open-forests and woodlands decreases steadily with increasing altitude. At the tree-limit (c.1220m), the mean height of the canopy is only 2m. Poorly drained to waterlogged sites between 910 and 1220m generally carry open-heaths, with a mean height somewhat less than 1m. Above 1220m, open-heaths and low shrublands, with a mean canopy height of less than 1m, occupy the entire range of drainage conditions. The mean height of the shrub stratum in these alpine communities decreases to less than 0.5m on waterlogged sites and on well drained to excessively drained sites at altitudes above c.1310m (Figure 8.1).

The total cover of all species occurring in a sample, which may be regarded as a crude indication of standing crop, also displays a reasonably well-marked pattern in relation to altitude and drainage (Figure 8.2). Mean total cover is maximal on moderately drained sites at altitudes less than 950m. Under these conditions, Eucalyptus subcrenulata open-forests, with a tall understorey of Leptospermum lanigerum and a dense low shrub stratum dominated by Bauera rubioides,

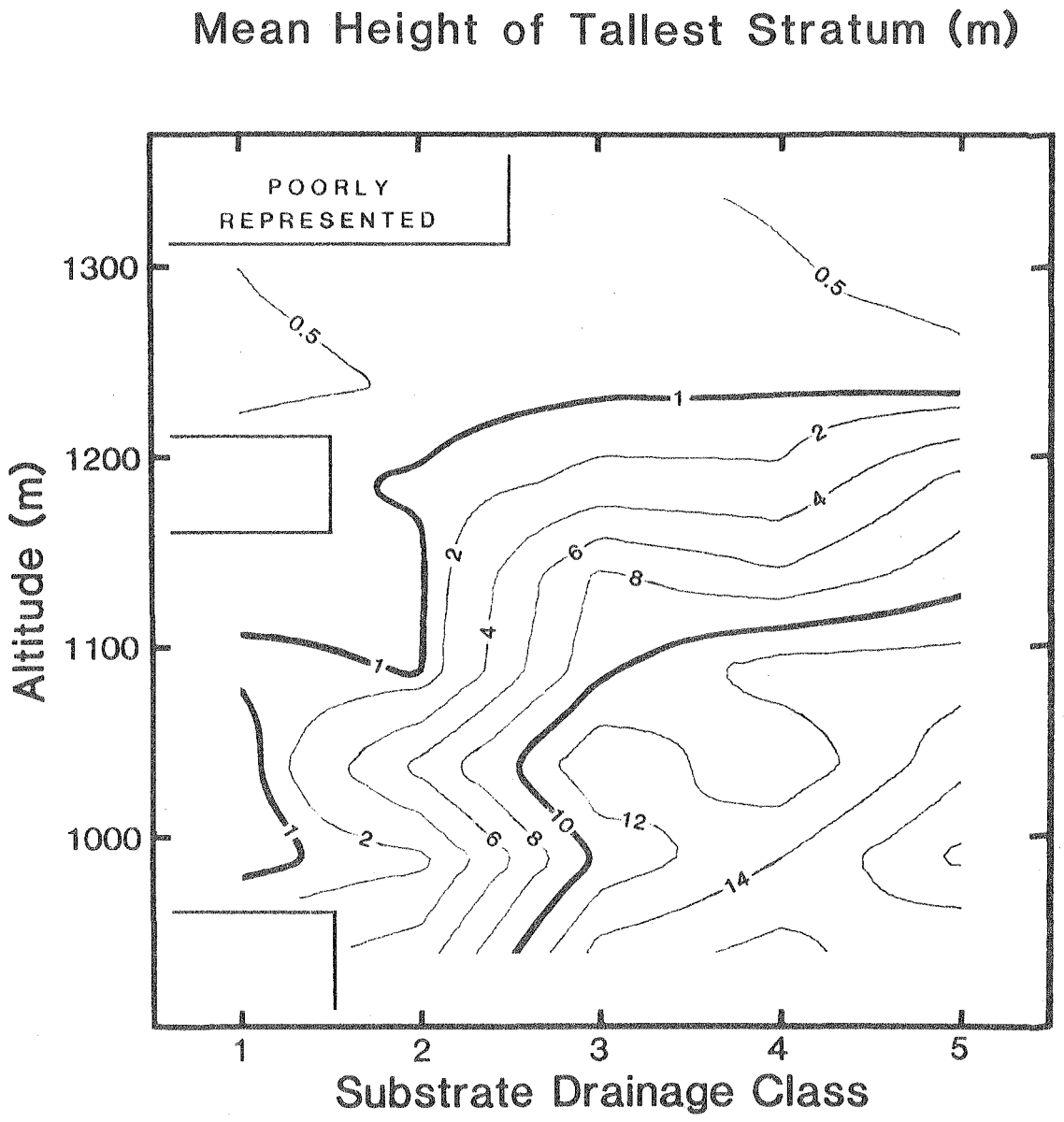


Figure 8.1 The trend surface, in relation to altitude and drainage, of the mean height of the tallest stratum (m).

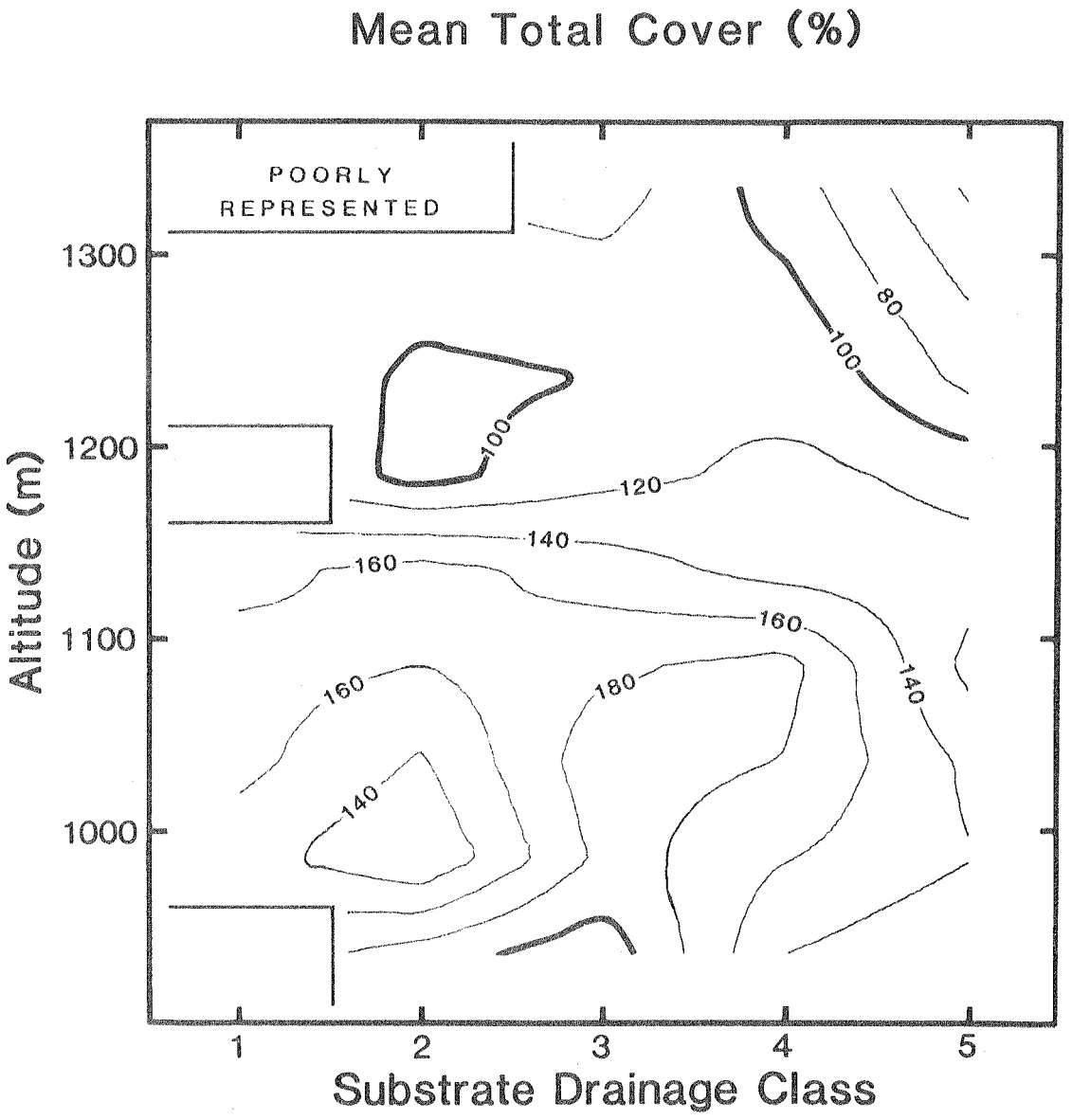


Figure 8.2 The trend surface, in relation to altitude and drainage, of mean total cover. Total cover, the sum of the percentage cover values for all species present in a sample, may be regarded as a crude index of standing crop, and hence a reflection of environmental carrying capacity.

attain a mean total cover of c.200%. At altitudes below 1100m, mean total cover decreases from moderately drained conditions towards both ends of the drainage gradient. The decline on poorly drained to waterlogged sites is associated with the elimination of tall shrubs and trees, while the decrease towards well drained sites and boulderfields reflects general decline in the cover of subordinate trees, tall shrubs and the ground layer. There is a general decrease in total cover with increasing altitude, with most of the alpine communities having a mean of c.100%. There is no abrupt decrease in total cover on moderately drained to excessively drained sites at the tree limit (c.1220m). In fact, the decline in total cover with altitude appears to be more abrupt in the open-heath communities on poorly drained sites (Figure 8.2). A marked decrease in total cover occurs on well drained to excessively drained sites at altitudes exceeding c.1250m. Boulderfields and screes at altitudes greater than 1300m usually carry low open-shrublands with a total cover of less than 50%.

Neither Simpson's index nor percentage dominance displayed systematic patterns with respect to altitude and drainage. Both these measures reflect the extent to which cover is equitably distributed among the species in a community. Mean values of Simpson's index ranged from 0.15 to 0.25, while the means for percentage dominance were generally between 45 and 55% throughout the ecoplane. However, both indices had exceptionally high values (0.42 and 72%) for boulderfields above 1300m. The low open-shrublands occupying such sites are often strongly dominated by Archeria sepyllifolia.

8.2.3.3 Patterns of Alpha Diversity

Figure 8.3 illustrates the trend surface, in relation to the altitude X drainage ecoplane, of alpha diversity (the mean number of vascular plant species per $100m^2$ sample). The shape of the surface is complex. The highest mean alpha diversity (32) is attained on waterlogged sites at altitudes between 1200 and 1260m. However, the trend surface has a long shoulder, extending towards well drained alpine sites. On moderately drained to excessively drained sites at altitudes less than c.1150m, mean alpha diversity is relatively constant, at 26-28 species per sample.

In an attempt to clarify the complex pattern of alpha diversity, the species were initially partitioned into woody and non-woody sub-sets. Contour diagrams showing the trend surfaces for the mean alpha diversity of these two fractions of the vascular flora are given in Figure 8.4. The pattern of alpha diversity was further clarified by the subdivision of woody and non-woody species into growth-form categories (Table 8.2). The allocation of species to these categories involved a degree of subjectivity. For example, Leptospermum lanigerum was classified as a tree, since it is single-stemmed and can exceed 5m in height under favourable conditions. However, on poorly drained and/or elevated sites it can be as low as 1m, and it might then be regarded as a shrub.

The response surfaces for the mean numbers of trees and erect shrubs per $100m^2$ sample are shown in Figure 8.4. The mean number of trees reaches a maximum of five in moderately drained to excessively drained sites at altitudes less than 950m. Tree diversity decreases

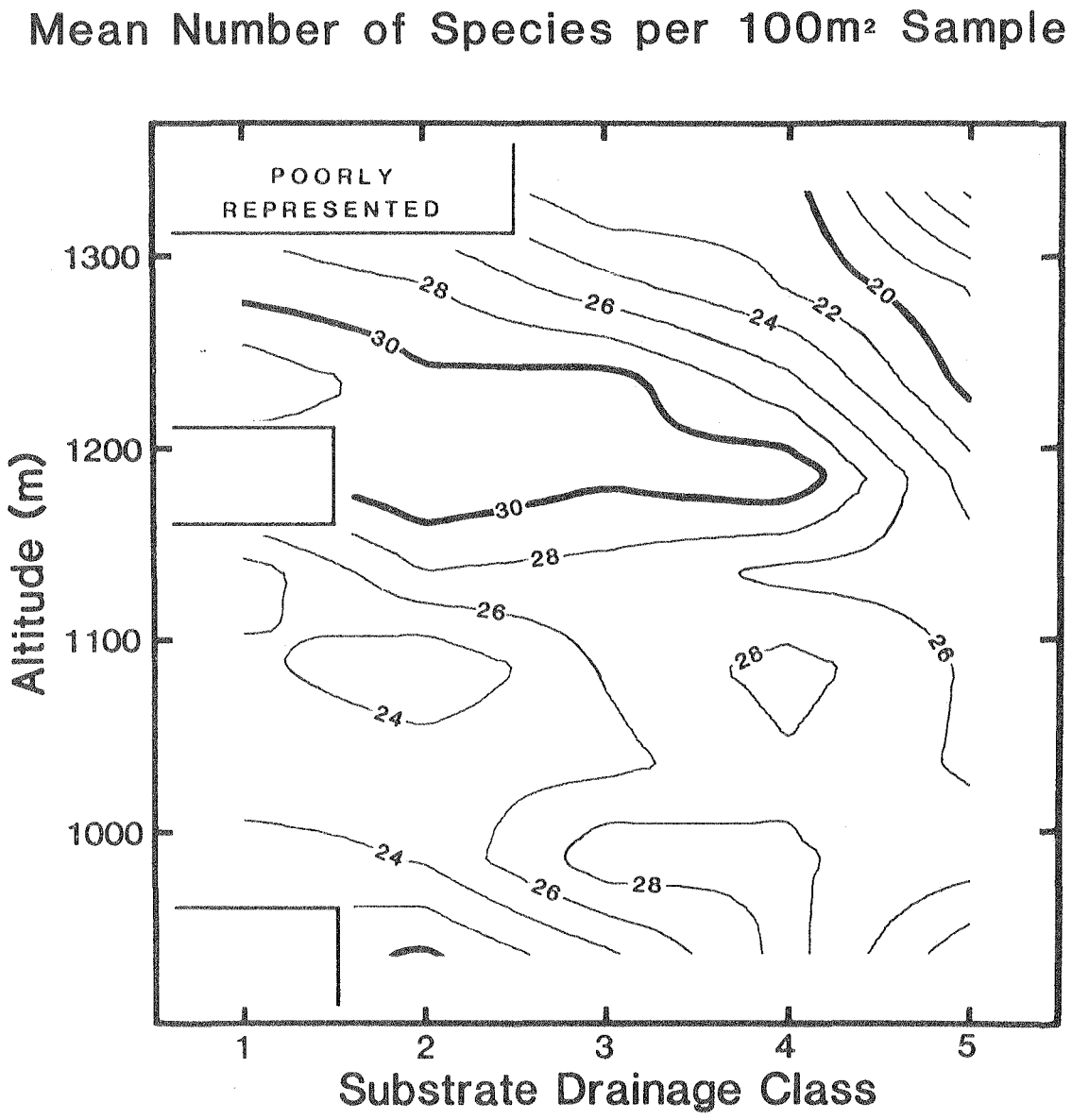


Figure 8.3 The trend surface, in relation to altitude and drainage, of the mean number of vascular plant species per 100m^2 sample.

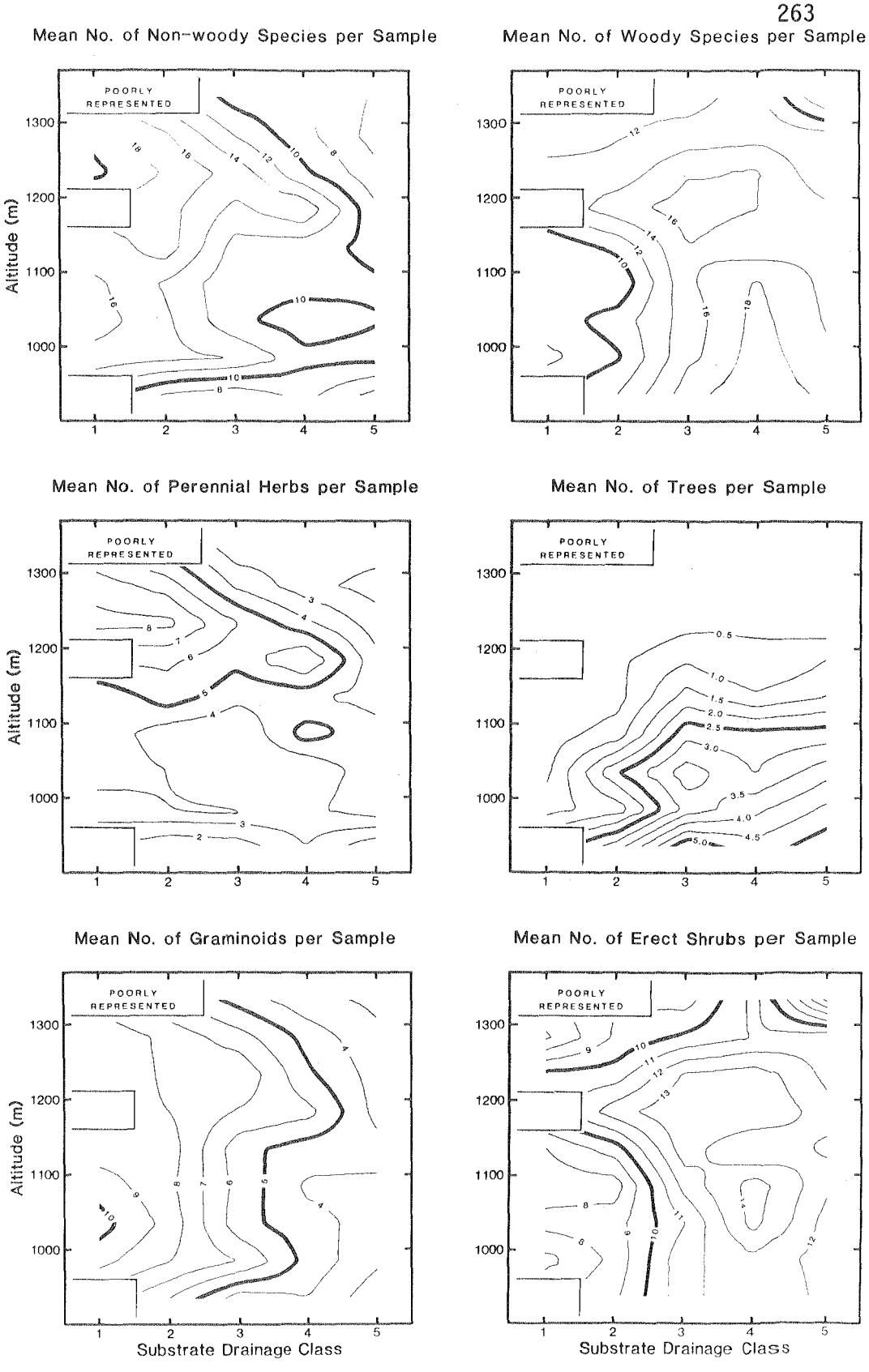


Figure 8.4 The trend surfaces, in relation to altitude and drainage, of the mean number of species in various growth-form categories per 100m^2 sample. The left-hand plots illustrate the diversity trends for non-woody species and the two major components of this group: perennial herbs and graminoids. At the right, the diversity trends for woody species and the two major component sub-groups, erect shrubs and trees, are shown.

steadily with increasing altitude, until at 1200m the mean number of trees per sample is less than one. Below 1100m, the mean number of trees declines markedly towards poorly drained and waterlogged sites. The trend surface for the mean number of erect shrubs has a peak of 14 on well drained sites at about 1150m, and shoulders extending towards well drained sites at lower altitudes and moderate to well drained sites at about 1220m. On boulderfields and screes, the mean number of erect shrubs per sample is relatively constant, at 11-12, from 930m up to almost 1300m. At higher altitudes, it declines rapidly, reaching a mean of six above 1350m. Below 1150m, the mean number of erect shrubs decreases towards conditions of poorer drainage, being only 7-8 on subalpine waterlogged sites. Above 1200m, there is a decline in erect shrub diversity with both increasing altitude and deteriorating drainage conditions.

The majority of non-woody species were classified as perennial herbs or graminoids (Table 8.2). The trend surfaces for the mean numbers of species per sample in each of these two categories are shown in Figure 8.4. Both surfaces appear to be unimodal, with the mean number of perennial herbs peaking at 8-9 in poorly drained and waterlogged sites at about 1240m and the mean number of graminoids reaching a maximum of 10-11 on waterlogged sites at about 1040m.

Thus the relatively complex pattern of total alpha diversity (Figure 8.3) can be understood in terms of the overlap of the simpler patterns exhibited by the different growth-forms. The alpha diversity of each growth-form group has a unimodal trend surface. However, the modes are located in different regions of the ecoplane. Peet (1978)

pointed out that the most successful studies of species diversity to date have concentrated on distinct functional groups of organisms, particularly birds. He suggested that plant species diversity may be more profitably approached in terms of component groups of directly competing species, possibly defined in terms of life-forms or growth-forms. The results of the present study show that even a relatively crude division of vascular plant species into growth-form categories can lead to a clarification of patterns of alpha diversity.

8.2.3.4 Between-habitat or Beta Diversity

Beta diversity values for the drainage gradient within five altitudinal belts and for the altitudinal gradient within each of the five drainage classes are given in Table 8.7. These values represent the estimated length of the gradients measured in units of half-changes of both the percentage similarity coefficient (PS) and its binary equivalent, Sorenson's coefficient of community (CC). Because the gradients were each divided into five relatively broad segments for the computation of beta diversity, the composite samples for the extreme segments do not express the composition of the vegetation right at the ends of the gradients. Hence the beta diversity values are likely to be underestimates. The absence of waterlogged and poorly drained sites at altitudes above 1300m means that the most elevated drainage gradient spans only three of the five drainage classes. For the same reason, the altitude gradients within drainage classes 1 and 2 are both truncated to only four steps. To facilitate comparisons between gradients, extrapolated beta diversity values are also given, in parentheses, for the truncated gradients. These were computed on the assumption that the ratio of the beta diversity of the missing

(a) Beta Diversities (half-change units) Based on the Percentage Similarity Coefficient (PS).

Altitudinal Gradients Within Each Drainage Class

	Substrate Drainage Class				
	1	2	3	4	5
All Species	2.55 (3.77)	2.81 (4.15)	3.25	3.79	3.51
Woody Species	2.80 (4.34)	2.73 (4.23)	3.42	3.76	3.56
Non-woody Species	2.39 (3.03)	2.93 (3.72)	3.05	4.46	3.93

Drainage Gradients Within Five Altitudinal Belts

	Altitude Range (m)				
	910-1010	1011-1110	1111-1210	1211-1310	>1310
All Species	4.02	3.34	3.59	3.13	1.67 (3.15)
Woody Species	3.94	3.44	3.57	2.97	1.63 (3.09)
Non-woody Species	5.02	3.93	3.91	3.94	1.90 (3.18)

(b) Beta Diversities (half-change units) Based on the Sorenson Coefficient of Community (CC).

Altitudinal Gradients Within Each Drainage Class

	Substrate Drainage Class				
	1	2	3	4	5
All Species	1.38 (2.28)	1.71 (2.83)	2.02	2.47	2.21
Woody Species	1.48 (2.52)	1.73 (2.95)	1.85	2.23	2.03
Non-woody Species	1.44 (2.28)	1.76 (2.78)	2.32	2.79	2.64

Drainage Gradients Within Five Altitudinal Belts

	Altitude Range (m)				
	910-1010	1011-1110	1111-1210	1211-1310	>1310
All Species	2.62	1.93	1.76	1.57	1.04 (1.96)
Woody Species	2.63	1.92	1.66	1.47	0.53 (1.18)
Non-woody Species	2.92	2.04	2.00	1.79	1.58 (2.68)

Table 8.7 Beta diversity values for the altitudinal and drainage gradients. The values are a measure of the total amount of compositional change along the gradients in half-change units (HC) based on (a) the percentage similarity coefficient (PS) and (b) Sorenson's coefficient of community (CC). Figures in parentheses are extrapolated values for the truncated gradients, the computation of which is explained in the text. For each gradient values were calculated using the data for all species, woody species only and non-woody species only.

segment(s) to total beta diversity for the truncated gradients was the same as that observed in the closest complete gradient of the same type.

Beta diversities of the altitudinal gradient, computed using data for all species, do not show any systematic trend with changing drainage conditions, whether based on percentage similarity (PS) or the Sorenson coefficient (CC). However, both sets of values suggest that altitudinal beta diversity is lowest in moderately drained sites (class 3), and highest (by extrapolation) in poorly drained sites (class 2). The beta diversities of the drainage gradients, based on PS, suggest a decline in beta diversity with increasing altitude, from approximately 4HC below 1010m to somewhat more than 3HC above 1210m. The corresponding set of values based on CC show a consistent decline over the first four altitude belts. However, the extrapolated value for altitudes greater than 1310m suggests an increase at the highest altitudes.

Whittaker (1960) noted a tendency for the beta diversity of forest vegetation along topographic moisture gradients to decrease with increasing elevation. In contrast, Peet (1978) found that beta diversity along topographic moisture gradients was lowest at intermediate altitudes, probably due to the suppression of understorey development by dominant conifers. Nevertheless, beta diversity of the most elevated topographic moisture gradients was considerably less than the beta diversity at the lowest altitudes.

Theoretical considerations (e.g. Whittaker 1972b) suggest that environmental instability, especially in the form of irregular or unpredictable fluctuations, should limit the development of beta diversity. Within the study area, the lowest altitude sites are

topographically sheltered from the full force of the prevailing west to south-westerly winds. It is therefore possible that the decrease in beta diversity along the drainage gradient with increasing altitude partly reflects an increasing degree of exposure to irregularly occurring storms. Another possible explanation for the higher beta diversity at lower altitudes is that the range of environmental variation along the drainage gradient is greater. Because of the rain-shadow effect of the higher ground to the west and south-west, plants growing on well drained sites and boulderfields in the lowest parts of the study area are more likely to experience a shortage of soil moisture than those at higher altitudes. Waterlogged conditions may also be more constant at lower altitudes, due to the greater catchment area above the subalpine moorlands in comparison with the elevated plateau surfaces (e.g. Mawson Plateau). These considerations highlight the fact that the scaling of environmental gradients in direct gradient analyses should ideally be based on measurements of habitat factors of direct operational significance to plants.

Beta diversity values for the altitude and drainage gradients, based on woody and non-woody sub-sets of the total flora are also given in Table 8.7. For the drainage gradients at all altitudes, the beta diversity based on non-woody species is always greater than the corresponding figure using woody species. Thus the degree of compositional change along the drainage gradient is greater among the herbs, graminoids and ferns of the ground layer than in the shrub and tree strata. Whittaker (1960) reported that beta diversity along topographic moisture gradients in the Siskiyou Mountains tended to increase from the highest to the lowest strata. The present results

provide some support for the concept that the beta diversity of gradients related to moisture supply may generally be greater for the lower strata. This trend may be related to the depth of rooting of different growth-forms. For shallow rooting grasses, sedges and forbs the effective range of moisture conditions along the drainage gradient may be greater than for the deeper rooting shrubs and trees. At the dry end of the gradient, the moisture conditions at depth are likely to be more constant than those near the surface.

Ogden and Powell (1979) studied the altitudinal trend in the diversity of woody species on the Mt. Field Plateau. Their approach was based on observations of the upper and lower altitudinal limits of woody species along the altitudinal "transect" provided by the Lake Dobson road, which extends from the National Park township (altitude c.160m) to the upper slopes of Mt. Mawson (altitude c.1220m). They regarded a given species as "potentially" present at any site between its observed altitudinal limits. In this manner, the "potential" richness of woody species at various altitudes was determined. The results suggested that the number of woody species reached a maximum of more than 60 at an altitude of somewhat more than 1000m and declined rapidly towards higher altitudes.

The published figure embodying the observations on which this analysis was based (Ogden and Powell 1979: Figure 2) contains several inaccuracies. Firstly, some of the species included have not been recorded on the Mt. Field massif by the present author and are also absent from the census of Davies (1978). These are probably the result of mis-identifications. Secondly, the upper and/or lower altitude

limits for many of the subalpine and alpine species are inaccurate to varying degrees. For example, the diagram places the upper altitudinal limit of such shrub species as Podocarpus lawrencii, Cyathodes dealbata, Orites acicularis, Olearia ledifolia, Richea scoparia, Orites revoluta, Coprosma nitida and Drimys lanceolata at 1260m. All of these species extend to an altitude of at least 1360m along the crest of the Rodway Range, the most elevated part of the present study area (see Appendices C and D).

However, the most serious problem with their analysis is that the "altitudinal" transect represented by the Lake Dobson road confounds variation in several other factors, including parent material, slope aspect and drainage. Within the present study area, the road transgresses sites representing all parts of the drainage gradient. The diversity values of Ogden and Powell (1979) therefore reflect not only variation in alpha (within habitat) diversity with altitude, but also the beta diversities along the other gradients represented at a given altitude.

Peet (1978) has argued strongly that, where alpha diversity is suspected of varying along several gradients, the appropriate observational approach should be multidimensional. Confounding of the effects of other gradients when sampling along a gradient of interest can lead to misleading or ambiguous results. The present study has shown that considerable floristic variation occurs along the drainage gradient in the lowest part of the present study area (910-1010m) and that beta diversity of the drainage gradient decreases with increasing altitude (Table 8.7). However, on the slopes of the plateau (below 910m), drainage conditions approaching those designated in the present

study as classes 1 and 2 are virtually absent. Hence the sudden rise in the number of woody species from 800 to 1000m, suggested by the analysis of Ogden and Powell (1979: Figure 3), is largely attributable to greater development of the drainage gradient and its associated compositional gradient on the plateau top.

The present results indicate that the patterns of alpha diversity on the Mt. Field Plateau are interpretable in terms of the current ecological responses of species to the altitudinal and drainage gradients (section 8.2.3.3). There is no need to invoke a complex historical explanation, involving speciation on the subalpine plateau during warming phases of the Pleistocene glaciation, as suggested by Ogden and Powell (1979).

8.2.4 Conclusion

Direct gradient analysis has shown that the alpine and subalpine plant communities of the Mt. Field Plateau form a compositional continuum in relation to the altitudinal and drainage gradients. The response surfaces of species to the ecoplane defined by these two major gradients can take a variety of forms, although most appear to be unimodal. A general discussion of the results will be deferred until after section 8.3, in which a more rigorous approach to the fitting of species response surfaces is examined.

8.3 The Use of Generalised Linear Modelling in Direct Gradient Analysis

8.3.1 Introduction

Austin and Cunningham (1981) stressed the need for more rigorous approaches to the problem of determining the form of species response curves along environmental gradients. The traditional technique of drawing a free-hand curve on a plot of species abundance versus position along a gradient, where the points represent either single samples or, more commonly, mean values for a number of adjacent samples (e.g. Whittaker 1956, 1960; Whittaker and Niering 1965; Westman 1975; Ogden and Powell 1979), has a number of serious shortcomings. The drawing of free-hand "curves of best fit" involves an inescapable element of personal bias. Unless some measure of the amount of scatter of individual observations around the curve is available, one can have little confidence in the adequacy of such a curve as a description of the relationship between species performance and the position of samples along the gradient. An examination of the few published figures in which individual data points are shown (e.g. Curtis and McIntosh 1951; Brown and Curtis 1952; Austin and Cunningham 1981) indicates that the amount of "residual" scatter around the fitted curves is generally large. This suggests a need for caution in the detailed interpretation of the shape of the fitted response curves.

Smoothing procedures based on weighted moving averages (Brown and Curtis 1952), or more complex non-linear smoothing methods (Austin and Austin 1980) may remove some of the subjectivity associated with the fitting of response curves. A major problem with such approaches is the need to provide arbitrary conventions for handling samples at the

extremes of gradients. Austin (1979) suggests that smoothing procedures based on running medians, rather than means, may be more robust against the "cascading effects" resulting from the application of end-point conventions with relatively short data sequences.

The division of gradients into segments, with subsequent computation of mean species performance within each segment, smooths out much of the variability between individual samples at any given point on the gradient. However, unless the total number of samples is extremely large, the width of the segments relative to the total length of the gradient may significantly reduce the precision with which the limits and modes of response curves can be located. Furthermore, different results may be obtained depending on the particular boundaries chosen for the segments.

A more satisfactory solution to the problem of defining species response curves or surfaces is the use of some type of regression procedure. The most widely used regression models assume that the distribution of errors (i.e. departures of the dependent variate from expectation based on the fitted model) is normal, with a mean of zero and a constant variance. However, a normal distribution of errors may not be appropriate for most measures of species performance or abundance (e.g. percentage cover, stem counts). In the case of stem counts, which are typically skewed to the left, with many zero values and few large values, Austin and Cunningham (1981) suggested that a Poisson or negative binomial error distribution may be suitable. For percentage cover, which is constrained between zero and 100, it seems reasonable to assume that the error variance associated with expected cover values

around 50% would be greater than the variance associated with expected values close to 0% or 100%. The appropriate error distribution for modelling of percentage cover may therefore be a continuous analogue of the binomial distribution.

Austin and Cunningham (1981) noted the existence of a more general class of regression models, known as Generalised Linear Models (GLM), details of which have been provided by Nelder and Wedderburn (1972). These models allow the error distribution of the dependent variable to have any specified form (e.g. Poisson, Binomial, Normal) They also permit the dependent variate and a linear combination of the predictor variables to be related by some chosen function, known as a link function. A generalised linear model is thus of the form: $f(y) = lp + e$, where y is the dependent variable, lp is a linear function of the predictor variables (whose parameters are to be estimated), e is a random error component (with some specified distribution) and f is the link function. Such models can be fitted by maximum likelihood methods. The familiar least squares regression models may be regarded as a special case of GLM, where e is normally distributed and f is the identity function.

Austin (1971) discussed several potential difficulties involved in the application of conventional regression methods in plant ecology. These include: (1) the non-normality of errors, (2) the dependence of the error variance on the values of the dependent or independent variables, (3) the existence of high correlations between independent variates (multicollinearity), (4) the lack of independence of the errors between observations and (5) the occurrence of numerous zero values of the dependent variable (species performance), some of which represent

totally unsuitable habitats. Most of the problems concerning the distribution of errors can be overcome by the use of GLM with a suitably chosen error function. Multicollinearity is best avoided by the judicious choice of the independent variables. Where functional relationships are known to occur among the "independent" variables, it is often useful to replace such variables by a synthetic variable derived from a suitable environmental process model (e.g. Austin 1971, 1979).

The zero value or "naughty nought" problem arises because species abundances are truncated at zero. When habitat conditions become too extreme for the survival of a species, its abundance drops to zero. As conditions depart even further from the limits of tolerance, no further reduction in abundance is possible. In other words, there is no measure of the "degree of absence" of a species. Attempts to fit a model for the abundance of a species which is absent over a considerable range of the values of one or more of the predictor variables, can lead to unsatisfactory results (e.g. Yarranton 1970). Austin (1971) tried to avoid the zero value problem by examining graphs showing the occurrence of the species of interest in relation to those environmental variables thought to be of importance. In this manner, it was possible to define an approximate domain in which the species could potentially occur. A more rigorous approach was introduced by Austin and Cunningham (1981). This involves the fitting of a predictive model for the probability of occurrence of a species, using GLM with a binomial error distribution and employing logit as the link function. Having obtained a model for probability of occurrence, those samples where the predicted probability of occurrence is greater than some arbitrarily selected value can be

selected as representative of a suitable domain for the modelling of abundance. This two-stage approach was adopted for use in the present study.

8.3.2 Methods

Practical considerations limited the fitting of response surfaces for probability of occurrence and percentage cover to a relatively small number of species. These included the eleven species designated as "major" (mean percentage cover in the modal cell greater than 20%) in the analysis of modal positions and heights (section 8.2.3.1). They were the trees Eucalyptus coccifera, E. subcrenulata and Leptospermum lanigerum, the shrubs Bauera rubioides, Orites revoluta, Richea sprengelioides, Epacris serpyllifolia and Helichrysum backhousii, the coniferous shrub Microstrobos niphophilus, the sedge Lepidosperma filiforme and the fern Gleichenia alpina. In addition, the shrub Orites acicularis, the lily Astelia alpina and the twining cord-rush (Restionaceae) Empodisma minus, whose response surfaces in the informal direct gradient analysis appeared to possess more than one peak (see Appendix C), were included in an attempt to obtain a more formal assessment of the reality of the apparent modes. Other species examined were the sclerophyll shrubs Archeria serpyllifolia and Drimys lanceolata, the coniferous shrub Podocarpus lawrencii and the prostrate conifer Microcachrys tetragona.

In the fitting of models for probability of occurrence, altitude and drainage were regarded as essential inclusions in the list of potential predictor variables. The previous informal analyses clearly indicated that all species display marked patterns of occurrence with

respect to these variables. Examination of the occurrence of species in relation to other environmental variables for which data was available (see sections 7.2 and 7.3) did not reveal any systematic relationships, except for variables functionally related to drainage (e.g. percentage rock cover, slope).

The two-way classification of samples, based on nine altitude classes and the five drainage classes (Table 8.1), was also used in modelling probability of occurrence. In each of the 41 occupied cells, the proportion of quadrats in which each species occurred was determined. Contours were fitted to the resulting grid of probabilities, using the computer program SURFACE II (Sampson 1978). These "observed probability of occurrence" diagrams were used to gain appreciation of the form of the response surfaces to be modelled.

For each species, a generalised linear model of the form logit(P)=linear function of predictor variables + binomial error term, where P is the probability of occurrence, was fitted using the general statistical program GENSTAT (Nelder et al. 1977). As predictor variables, various combinations of altitude (midpoint of altitude class), drainage (integer class value), altitude^2, drainage^2 and altitude X drainage were examined. The product term was included to allow for the possibility that the probability of occurrence surfaces might be rotated with respect to the altitude and drainage axes. Squared and/or product terms were only included if they led to a significant reduction in the residual mean deviance. The fitting of a quadratic model with a logistic link function results in a symmetrical, bell-shaped surface. A logistic model with only linear terms produces a

sigmoid curve or surface. For binomial GLM's, the residual deviance may be employed as a goodness-of-fit statistic. On the assumption that the model fits perfectly, the residual deviance is distributed approximately as Chi-squared, with the residual degrees of freedom (i.e. number of observations - number of fitted parameters -1) (Nelder and Wedderburn 1972).

Using the fitted equations, a grid of expected probability values was computed for each species, and contour diagrams representing the fitted probability of occurrence surfaces were prepared using the program SURFACE II (Sampson 1978). The residuals were examined in relation to altitude and drainage, to see if they formed any systematic pattern which would suggest that the shape of the fitted surface was inappropriate.

For each species, those samples where the expected probability of occurrence (based on the fitted binomial model) was less than 0.1 were excluded when attempting to fit a model for percentage cover. In addition, the 14 samples with heterogeneous drainage conditions, 20 samples subjected to wild-fires in the 1960s and seven samples with annual radiation estimates less than 11 kJ/cm^2 were excluded from the regressions for all species.

The results of the informal direct gradient analysis (section 8.2), have shown that both altitude and drainage to have a strong, generally curvilinear, effect on the mean percentage cover of all species. Hence altitude, altitude^2, drainage, drainage^2 and altitude X drainage were included as potential predictor variables. Estimated annual solar radiation was also tried, since variation in cover with

aspect was suspected for some species. Models of the form C=linear function of predictor variables + e, where C is the percentage cover and e is an error term, were fitted. Due to limitations in the flexibility of the available software, a normal distribution of errors was assumed, even though theoretical considerations suggested that the appropriate error distribution for percentage cover may be of some other form (see section 8.3.1).

In fitting both the binomial and normal models, decisions concerning the inclusion or exclusion of individual terms were based mainly on whether or not the inclusion of the term resulted in a marked decrease in the residual mean deviance or residual mean square, respectively. The t tests based on estimates of the standard errors of parameters were used as a rough guide only, since the standard error estimates may be biased when the assumptions concerning the distribution of errors are not fully justified.

To assess the adequacy of the normal models, the percentage of the total variance accounted for by the model was computed as ((total variance -residual variance) /total variance)x100%. This is not the same as the coefficient of determination (r^2), which is calculated using sums of squares rather than mean squares (variances). The expression based on variances was preferred, since it corrects for the number of degrees of freedom available. In any case, since the number of observations in most analyses was greater than 100, the difference between the values of the two expressions was usually small.

For most species, the final model only contained terms related to altitude and drainage. In such cases, the fitted equations were used to

compute a grid of expected cover values to which contours were fitted using the program SURFACE II (Sampson 1978). Where a radiation term proved to be necessary, a grid of expected cover values in relation to altitude and drainage was calculated at each of several radiation levels and contours were fitted to each grid.

The residuals from the fitted cover models were subjected to several analyses. Firstly, the product-moment correlation between the absolute values of the residuals and their associated fitted cover values was computed. A significant correlation would suggest that the variance of the residuals is not independent of the magnitude of the fitted value, as assumed by the normal regression model. A second analysis was designed to assess the proportion of the residual sum of squares which might be attributable to the use of fairly coarse classes for cover observations. For example, suppose that the expected percentage cover in a particular sample was 30%. In that case, the closest possible observed value, given the system of classes employed (Table 7.1), would be 20% (i.e. midpoint of class 4). For each sample, the nearest possible observed cover value to the value predicted by the fitted model was determined and the sum of the squares of the deviations between these "best possible" observations and expectation was computed. This sum of squares was then subtracted from the residual sum of squares, to produce an adjusted value, expressing the degree of departure from expectation beyond that attributable to the use of coarse cover classes. The adjusted residual sum of squares was divided by the residual degrees of freedom to obtain an adjusted residual mean square which, in turn, was used to derive an adjusted estimate of the percentage of the total variance accounted for by the model.

The third approach to the analysis of the residuals was an examination of their distribution with respect to altitude and drainage. For each species, the samples used for the the modelling of percentage cover were classified according to altitude and drainage, using the classes shown in Table 8.1. Within each cell, the mean, standard deviation, minimum and maximum of the residuals was computed. If the shape of the fitted response surface were inappropriate, this would be indicated by the occurrence of adjacent blocks of cells with mean residuals consistently greater or less than zero.

8.3.3 Results

Contour diagrams illustrating the observed and fitted response surfaces for both probability of occurrence and percentage cover are presented for 18 selected species in Appendix D. The observed percentage cover diagrams for these species were previously given in Appendix C. They are repeated here for ease of comparison with the fitted response surfaces.

The fitted equations for the probability of occurrence surfaces, together with the residual deviances and the results of the approximate Chi-squared goodness-of-fit tests, are given in Table 8.8. Most species required both altitude and altitude^2 terms, indicating a non-monotonic relationship between probability of occurrence and altitude. The only exception was Archeria serpyllifolia which is restricted to the highest altitudes. The shape of the truncated probability surface for this species, with respect to altitude, was adequately fitted using a simple altitude term only. Species reaching their maximum probability of occurrence at either extreme of the drainage gradient (i.e. class 1 or

Species	Fitted Binomial Model for Probability of Occurrence	Residual Deviance	Residual d.f.	Probability
Archeria serpyllifolia	logit(P)[1]= -60.9 +0.0368A +6.27D -0.704D^2	12.27	36	0.9999
Astelia alpina	logit(P) = -33.0 +0.0587A -0.0000225A^2 -0.776D	39.69	36	0.3089
Bauera rubioides	logit(P) = -91.0 +0.189A -0.0000994A^2 -1.87D -0.447D^2 +0.00435AD	39.21	34	0.2476
Drimys lanceolata	logit(P) = -89.3 +0.144A -0.0000592A^2 +4.57D -0.00273AD	48.05	35	0.0698
Empodisma minus	logit(P) = -0.960 +0.0329A -0.0000235A^2 -5.18D +0.00307AD	46.83	35	0.0872
Epacris serpyllifolia	logit(P) = -68.8 +0.141A -0.0000658A^2 -5.19D +0.00349AD	61.30	35	0.0039
Eucalyptus coccifera	logit(P) = -163.9 +0.301A -0.000143A^2 +3.04D -0.273D^2	47.65	35	0.0752
Eucalyptus subcrenulata	logit(P) = -85.0 +0.167A -0.0000871A^2 +2.75D -0.348D^2	41.06	35	0.2221
Gleichenia alpina	logit(P) = -148.3 +0.293A -0.000140A^2 -1.73D	33.42	36	0.5919
Helichrysum backhousii	logit(P) = -125.4 +0.166A -0.0000531A^2 +9.32D -0.304D^2 -0.00595AD	45.32	34	0.0928
Lepidosperma filiforme	logit(P) = -132.3 +0.272A -0.000135A^2 -1.56D	20.63	36	0.9812
Leptospermum lanigerum	logit(P) = -172.4 +0.362A -0.000191A^2 -3.29D -0.430D^2 +0.00571AD	30.73	34	0.6287
Microcachrys tetragona	logit(P) = -254.1 +0.399A -0.000157A^2 +1.19D -0.319D^2	31.94	35	0.6166
Microstrobos niphophilus	logit(P) = -103.0 +0.167A -0.0000673A^2 +0.493D -0.233D^2	71.60	35	0.0003
Orites acicularis	logit(P) = -37.2 +0.0546A -0.0000188A^2 +0.605D -0.190D^2	45.94	35	0.1021
Orites revoluta	logit(P) = -54.5 +0.0826A -0.0000329A^2 +3.11D -0.458D^2	84.23	35	<0.0001
Podocarpus lawrencii	logit(P) = -217.4 +0.347A -0.000140A^2 +0.787D	23.71	36	0.9424
Richea sprengelioides	logit(P) = -63.1 +0.0920A -0.0000357A^2 +3.47D -0.461D^2	62.24	35	0.0031

[1]logit(P) = log (P/(1-P)).

Table 8.8 Binomial models for the probability of occurrence (P) of 18 selected species. The models were fitted using Generalised Linear Modelling with a binomial error distribution and logit as a link function. In the equations, A represents altitude (m) and D stands for drainage expressed as an integer class value. Residual deviances are based on a scale factor of 1.0. For binomial GLMs the residual deviance can be used as a goodness-of-fit statistic, approximately distributed as Chi-squared. The probabilities resulting from these goodness-of-fit tests are given in the rightmost column.

5) similarly required only a drainage term, while those attaining their maximum probability of occurrence under intermediate drainage conditions needed a drainage^2 term as well. For six species, the fit of the probability surface was significantly improved by the introduction of a product term, which allowed the fitted surface to be rotated with respect to the altitudinal and drainage axes.

Goodness-of-fit tests, based on the residual deviance, indicated that the models for all but four of the species fitted adequately at the 5% significance level. The species for which an acceptable fit was not achieved were Epacris serpyllifolia, Orites revoluta, Richea sprengelioides and Microstrobos niphophilus. The first three of these occur over a very wide range of altitude and drainage conditions within the study area, as shown by the observed probability of occurrence diagrams in Appendix D. The distribution of the residuals for these three species with respect to altitude and drainage displayed marked patterns, which suggested that the underlying probability of occurrence surfaces were not adequately fitted by a unimodal, symmetrical model. For Orites revoluta a bimodal surface was indicated. Both Epacris serpyllifolia and Richea sprengelioides appeared to have unimodal probability surfaces, with broad modes in the approximate positions indicated by the best fitting models, but the "slopes" of the surfaces seemed to be fluted, rather like the stream-dissected slopes of a mountain. Microstrobos niphophilus, the other species for which no adequate binomial model was found, seemed to require a sharply ridged probability surface, skewed towards lower altitudes. Although the best fitting binomial models for these four species (as illustrated in Appendix D) cannot be regarded as accurate representations of the

underlying probability of occurrence surfaces, they were nevertheless considered adequate for the purpose of identifying samples with "unsuitable" habitats, which should be excluded from attempts to model percentage cover.

The fitted models for percentage cover of the 18 species, based on least squares multiple regression, are given in Table 8.9. In most cases, the F ratio tests (regression mean square /residual mean square) left no doubt that the fitted response surface was a significant improvement on the null hypothesis of equal mean cover over all values of the predictor variables. However, in most cases the percentage of variance explained is not impressive. Only five of the models accounted for more than 30% of the total variance, while six species had values less than 15%. The most predictive model was that for the fern Gleichenia alpina, which accounted for 46.6% of the total variance. Adjustment of these values to take into account the limited precision of measurement (section 8.3.2), resulted in a reasonable improvement for most species. Nine species had adjusted values greater than 30% and only three, Microcachrys tetragona, Orites acicularis and Orites revoluta, still had values less than 15%. Nevertheless, it is clear that a considerable scatter of observations around the fitted response surfaces occurs for all species.

All the fitted equations included terms for both altitude and drainage, with most species requiring an additional squared term for one or both of these. Only Eucalyptus subcrenulata benefitted significantly from the inclusion of a solar radiation term. For both Astelia alpina and Empodisma minus, only simple altitude and drainage terms were

Species	Fitted Normal Model for Percentage Cover	Number of Samples Used	Percentage[1] of Variance Explained(PV)	PV Corrected[2] for Cover Class Effect	F	Probability
Archeria serpyllifolia	$C = -166.5 + 0.109A + 15.4D - 1.85D^2$	91	31.7	47.1	15.0	<0.0001
Astelia alpina	$C = -12.4 + 0.0279A - 3.55D$	397	16.2	24.6	39.3	<0.0001
Bauera rubioides	$C = -70.9 + 1.36A - 0.000685A^2 + 4.36D - 6.51D^2$	283	35.0	43.6	39.0	<0.0001
Drimys lanceolata	$C = -121.0 + 0.207A - 0.0000902A^2 + 1.79D$	382	33.5	44.1	64.8	<0.0001
Empodisma minus	$C = 40.3 - 0.0238A - 2.81D$	309	20.9	32.1	41.7	<0.0001
Epacris serpyllifolia	$C = -267.3 + 0.488A - 0.000211A^2 + 3.07D - 1.03D^2$	390	18.3	32.1	22.8	<0.0001
Eucalyptus coccifera	$C = -511.1 + 0.974A - 0.000475A^2 + 9.29D$	237	24.2	36.5	26.1	<0.0001
Eucalyptus subcrenulata	$C = -62.8 - 0.0800A + 21.5D - 2.74D^2 + 7.77R$	150	20.1	27.6	10.4	<0.0001
Gleichenia alpina	$C = -1299.4 + 2.52A - 0.00117A^2 - 16.5D$	152	46.6	55.1	44.9	<0.0001
Helichrysum backhousii	$C = -134.6 + 0.102A + 26.2D - 1.16D^2 - 0.0144AD$	270	19.9	26.7	17.7	<0.0001
Lepidosperma filiforme	$C = -588.5 + 1.24A - 0.000625A^2 - 9.49D$	134	28.0	33.2	18.2	<0.0001
Leptospermum lanigerum	$C = -1387.5 + 2.71A - 0.00135A^2 + 35.4D - 5.75D^2$	187	35.0	43.8	26.1	<0.0001
Microcachrys tetragona	$C = -58.0 + 0.0498A + 1.52D - 0.466D^2$	133	4.6	7.3	3.1	0.0291
Microstrobos niphophilus	$C = -520.2 + 0.783A - 0.000277A^2 + 32.5D - 0.0304AD$	229	15.2	18.8	11.2	<0.0001
Orites acicularis	$C = -6.49 + 0.00584A + 2.97D - 0.551D^2$	364	3.8	10.9	5.8	0.0007
Orites revoluta	$C = -145.3 + 0.243A - 0.000105A^2 + 5.52D - 0.692D^2$	396	10.5	12.7	12.6	<0.0001
Podocarpus lawrencii	$C = -421.3 + 0.667A - 0.000266A^2 + 2.35D$	224	11.5	16.4	10.7	<0.0001
Richea sprengelioides	$C = -255.6 + 0.420A - 0.000178A^2 + 8.28D - 0.938D^2$	366	11.4	16.8	12.8	<0.0001

[1]Based on mean squares, rather than sums of squares.
[2]Derivation of these values is explained in the text.

Table 8.9 Fitted equations for percentage cover (C) of 18 selected species. The models were fitted using least-squares multiple regression, which assumes a normal distribution of errors. In the equations, A represents altitude (m), D represents drainage (integer class value) and R represents estimated annual solar radiation (kJ/cm^2). For each species, only those samples where the expected probability of occurrence, based on the previously fitted binomial model, was at least 0.1 were included. Approximate F ratio tests for the significance of the entire regression are given in the rightmost two columns.

justifiable, hence the fitted response surfaces for these two species are sloping planes.

In all cases, there was a significant positive correlation between the absolute values of the residuals and expected percentage cover. This casts doubt on the assumption that errors are normally distributed, with a variance independent of the expected value. It was suggested above (section 8.3.1) that an appropriate error distribution for measures such as percentage cover might be a continuous analogue of the binomial distribution, with values around 50% being subject to greater variation than both high and low values. In the present examples, expected cover values were always less than 50%, hence a monotonic increase in the error variance with increasing expected cover would be expected. The system of cover classes employed may also have contributed to the correlations between the absolute values of the residuals and expected cover, since the spacing between class midpoints is greater for the higher cover classes.

An examination of the distribution of the residuals with respect to altitude and drainage revealed systematic patterns for some species. For both Astelia alpina and Empodisma minus, two regions with a preponderance of positive residuals occurred, separated by a zone where mean residuals were negative. The response surfaces for these two species were classified as bimodal in the informal direct gradient analysis (section 8.2.3.1). The observed patterns in the residuals support this view. Hence the fitted planar response surfaces must be regarded as over-simplifications. On the other hand, no pattern could be discerned in the residuals for Orites acicularis, the other species for which the informal direct gradient analysis suggested a complex

response surface. Consequently, a broad, unimodal response surface may be accepted as a reasonable model for this species, although the scatter around the surface is so great that, even after correction for the use of cover classes, the model has little predictive value.

For several species whose percentage cover model included only a simple linear term for either altitude or drainage, patterns in the residuals suggested that a sigmoid rather than linear shape with respect to that predictor would have been more appropriate. For example, mean residuals for Drimys lanceolata are positive near its mode. Moving away from the mode towards poorer drainage one passes through a zone where mean residuals are negative and then, under poorly drained and waterlogged conditions, mean residuals are positive again. This indicates that the decline in percentage cover with deteriorating drainage conditions may be better modelled by a sigmoid, or at least concave surface, rather than the plane implied by the fitted model.

8.3.4 Discussion

The present results indicate that Generalised Linear Modelling is a promising approach to the formalisation of direct gradient analysis. The initial fitting of a binomial model for probability of occurrence provides an objective procedure for reducing the problems caused by numerous zero values (Austin and Cunningham 1981). It allows samples where the expected probability of occurrence of a species is low to be identified and excluded from quantitative regressions. Although the definition of an appropriate domain for modelling of species abundance was the primary reason for the fitting of binomial models in the present study, the fitted binomial models were also of some intrinsic interest.

They indicated that the relationship between probability of occurrence and the environmental plane defined by altitude and drainage may be adequately represented by a unimodal, symmetrical response surface, for all but four of the species examined. The scatter of observations (i.e. cell frequencies) around the fitted surfaces, as expressed by the residual deviances, was reasonably small in most cases. This may be contrasted with the generally high levels of residual variation in the percentage cover models for these species.

A simple model of species occurrences along an environmental gradient (cf. Prentice 1980) is for each species to be confined to a limited region of the gradient, being present with a constant probability (P) within that region and absent in all other parts of the gradient. If such a model applied, adequately fitting probability profiles would be step-functions, with values of zero outside the region of occurrence and P within that region. However, the present results suggest that probability of occurrence is smoothly related to environmental gradients. There are no sharp boundaries between favourable and unfavourable regions of the gradient. Rather, there appears to be a gradual decline in probability of occurrence as one moves away in either direction from some optimal point.

There are at least three possible explanations for the gradually tapering forms of the probability profiles, and these are not mutually exclusive. Firstly, the presence or absence of species may partly reflect the operation of stochastic processes, which can eliminate or prevent establishment of species on certain sites. A given species may be absent from a site where conditions are generally suitable for its

growth because of the chance occurrence of some event in the past. The fortuitous proximity of a mature, seed-bearing individual at a time when the vegetation on a site was disturbed may ensure that the species is present in the regenerating vegetation. If disturbance occurred at at a time when seed was not available, the species may be eliminated from the site, at least temporarily. Suppose that there is some point along an environmental gradient where conditions are optimal for the establishment, growth and reproduction of a species. It seems reasonable to postulate that the chance of the species being eliminated, or prevented from establishment by the operation of stochastic processes would be minimal in sites located at that point. As one moves away in either direction, towards less favourable conditions, the probability of absence due to stochastic events may be expected to increase. Likely causes of such stochastic variation on the Mt. Field Plateau are wild-fires and exceptionally severe frosts.

Another possible explanation for the tapered probability of occurrence profiles is the effect of other "lurking factors" which are at least partially independent of the environmental complex-gradients used for direct gradient analysis. The effects of these other factors on the performance of a species may be sufficiently great to render unsuitable sites which would otherwise be considered, on the basis of the major gradients, to be suitable habitats for that species. Species absences due to the effects of such lurking factors may be expected to become more frequent with increasing departure from the optimum of the species along the recognised gradients. The decline in performance associated with increasingly sub-optimal conditions on the major gradients makes it more likely that a further reduction in performance

due to sub-optimal levels of some lurking factor(s) will be sufficient to lead to the elimination of the species.

A third possible reason for the tapering probability of occurrence profiles is related to sampling and spatial pattern. Where conditions are optimal for the growth of a species, it may be represented by a sufficiently high density of individuals that samples of a given size located in the community will almost certainly contain at least one individual. As conditions become less optimal, the spatial distribution of the species may become increasingly sparse and patchy. Samples of a given size will then be increasingly likely not to include any individuals of the species, even though it is present in the community.

Whatever its origin, the recognition that there is often a strong systematic relationship between probability of occurrence of species and positions of samples along major environmental gradients has important implications for the design and evaluation of procedures for indirect gradient analysis (see Part 1 of this thesis).

For most species, attempts to fit a predictive model for percentage cover were less successful than the corresponding binomial models. Prime examples are Microcachrys tetragona and Orites acicularis, whose percentage cover models accounted for only 4.6 and 3.8% of the total variance, respectively. There are a number of factors which may have contributed to the large residual variances for most species. These include (1) the use of an inappropriate error distribution, (2) failure to specify the correct functional form for the relationship between percentage cover and the predictors, (3) the use of fairly coarse and unequally spaced cover classes, (4) inadequacy of

altitude and/or drainage scores as indices of position on the perceived major gradients, (5) the failure to include some important predictor(s) in the model, (6) possible variations in cover due to stochastic processes and (7) sampling errors associated with spatial patterning.

The probable inappropriateness of a normal error distribution for percentage cover has been mentioned previously. The flexibility of Generalised Linear Modelling allows considerable freedom in the specification of error distributions, so this problem should be surmountable once the appropriate distribution has been identified. Generalised Linear Modelling permits some flexibility in defining the form of the relationship between the dependent variable and the linear function of predictors through the choice of a link function. In the present models, the use of the identity function as a link function and simple linear, squared and product terms for the predictors, permitted only planar or parabolic forms for the fitted response surfaces. For several species, patterns in the residuals suggested that sigmoid or bell-shaped surfaces would have been more adequate. Most of the 18 species for which modelling was attempted appeared to have symmetrical, unimodal response surfaces.

Where the response surface for a species with respect to some predictor appears to be skewed, one possible approach is to pre-transform the predictor variable. For example, the inclusion in models of square root and simple linear terms for some predictors by Austin (1971) and Austin and Cunningham (1981) is equivalent to pre-transforming those predictors to a square root scale, then fitting a quadratic for the transformed predictors. This allows the fitted curve be positively skewed (i.e. skewed to the left). Another possibility,

where a positively skewed relationship is suspected, would be to transform the predictor to a log scale. Where negatively skewed relationships occur, the "direction" of the predictor may be reversed by subtracting its values from some chosen upper bound and an appropriate transformation may then be applied to the resulting complements (cf. Fresco 1982).

Gauch and Chase (1974) developed a "variation of parameters" algorithm which fits a Gaussian curve to the relationship between a dependent variable and a single predictor variable. Maximum likelihood estimates of the parameters of the Gaussian curve are determined by an iterative process and the resulting curve approaches the best possible least-squares fit. Their method has been used to fit Gaussian response curves by Westman (1980) and Werger, Louppen and Eppink (1983). A major limitation of the approach is that only one predictor is allowed. Algorithms for the direct fitting of Gaussian surfaces or hypersurfaces, for the relationship between a dependent variable and two or more predictors, do not appear to be available.

An alternative approach to the modelling of species response is to divide each predictor variable into classes, and fit a parameter for each class (Austin, Cunningham and Good 1983). This does not require the prior specification of the functional form of the relationship. Even bimodal responses can readily be handled by such an approach.

The use of cover classes rather than more continuous estimates of cover in the present study has been justified primarily on practical grounds. It was also felt that much of the relevant "information" on the compositional variation of the vegetation as a whole would be

captured using cover classes. Nevertheless, for the purpose of detailed studies of the shape of the response curves (surfaces) of individual species along gradients, a more continuous abundance scale would be desirable. In future direct gradient studies a compromise may have to be sought between the need to obtain an adequate number of samples and the increase in sampling time and effort necessary for precise measurements of species performance.

The present approach to direct gradient analysis assumes that values of the predictor variables are not subject to sampling error. However, this is unlikely to be true. Errors in the specification of altitude, radiation and especially drainage scores for individual sites probably contributed to the large residual variances obtained in most of the cover regressions. The lack of an easily measured index of position on the drainage gradient necessitated the use of a relatively crude, five point scale. Despite attempts to specify rigorous criteria for assignment of sites to these drainage classes (see section 7.2), an element of subjectivity was probably involved in the assignment of "borderline" cases. Scaling of the drainage gradient assumes that the degree of "environmental variation" between each pair of adjacent classes is equal. However, this assumption may be questioned.

Stochastic variations in cover, due to irregularly occurring events, are a possible source of residual variation which cannot be overcome by improvements in sampling and measurement methods. Different chance events may affect the abundances of different species growing on the same sample area. Species specific attack by insects, herbivores or disease organisms are possible examples.

The present models do not allow for the possibility of interaction between species, due to competitive modification of available resource levels or more direct effects, such as allelopathy or parasitism. One approach to this question is to include the abundances of other species as predictors (cf. Austin and Cunningham 1981). This was tried for several species in the present study, but no improvement in the predictive value of the models was noted.

One other potential source of residual variance is sampling error, due to the spatial patterns of various species and the size and shape of the sample area employed. The size of the sample compared with the mean size and spacing of individual plant canopies is an important consideration. If the sample size is small in relation to plant size, a high sampling variance may result. Large cover values will occur when the sample falls, by chance, on a plant canopy and low values where the sample is located in a gap. The $100m^2$ rectangular samples used in the present study were sufficiently large with respect to most shrubs and non-woody species to reduce the likelihood of high sampling variance due to spatial exclusion effects. However the possibility cannot be ruled out that this type of sampling error may have been important for the larger tree species, especially Eucalyptus coccifera and E. subcrenulata.

The relatively large residual variances observed for most of the 18 species for which modelling was attempted may therefore be attributable to a number of factors. The effects of some of these may be reduced by methodological improvements, both in sampling and in the specification of the models.

The present study supports the suggestion of Austin and Cunningham (1981) that Generalised Linear Modelling is a useful approach to the formalisation of direct gradient analysis. Unlike free-hand curves, the response curves (or surfaces) derived by GLM are repeatable. The fitted parameters are maximum likelihood estimates and the residual deviance provides an indication of the adequacy of the fitted model as description of the observed relationship. The use of statistical methods such as GLM is essential if rigorous observational evidence concerning the form of species response curves (surfaces) along gradients is to be obtained. The present author agrees with Austin and Cunningham (1981) that "smoothed curves without data points are no longer enough".

8.4 General Discussion and Conclusions

One of the major contributions of direct gradient analysis to the development of ecological theory has been a clearer understanding of the manner in which species populations are organised into communities, through their patterns of response to underlying environmental gradients and mutual interactions (Whittaker 1978a). The general picture which has emerged from the results of direct gradient analyses (see reviews by Whittaker 1967, 1978a and McIntosh 1967) is in accordance with the "individualistic hypothesis" of Gleason (1926, 1939). Along a single environmental gradient, the abundance profiles of species are often unimodal, with each species appearing at a given point on the gradient, rising in abundance to some maximum value, then declining again to absence. Although the response curves sometimes appear to be bell-shaped and more or less symmetrical, other shapes, including

skewed, shouldered, flat-topped, bimodal or multimodal forms have also been commonly observed. As predicted by the individualistic hypothesis, pairs or groups of species with very similar patterns of distribution along gradients are seldom encountered. In contrast, the limits and modes of species abundance profiles appear to be randomly scattered, with the exception that major species modes sometimes appear to be more evenly spaced (Gauch and Whittaker 1972a). When two or more gradients are considered simultaneously, species response surfaces or hypersurfaces are generally found to be convex and bell-shaped, though not necessarily symmetrical. The patterns of compositional variation resulting from the overlapping abundance profiles of individualistically distributed species are continuous. Thus the vegetation of a relatively undisturbed landscape may generally be visualised as a compositional continuum, any dissection of which is essentially an arbitrary process (Whittaker 1978a).

The results of the present study suggest that the subalpine and alpine vegetation of the Mt. Field Plateau may be visualised as a two-dimensional compositional continuum, resulting from the overlapping individualistic distributions of species along the two major complex-gradients related to altitude and drainage. The response surfaces for mean percentage cover of individual species, examples of which are given in Appendix C, are regarded as "ecological response surfaces" in the sense of Ellenberg (1953). They reflect both the physiological responses of species to the environmental variables of the altitudinal and drainage complexes and the possible effects of interactions between species. Such interactions potentially include those commonly labelled as "competition", as well as other types of

interspecific interference such as allelopathy and parasitism. This study does not provide any information about the levels of interference between species or the relative importance of possible mechanisms for such interference. These questions are best studied experimentally (e.g. Ellenberg 1953, 1954; Austin and Austin 1980). However, Fresco (1982) has presented a numerical approach which attempts to deduce sets of "physiological" response curves and linear interference coefficients which could have given rise to a set of observed ecological response curves. When studying the ecological response of species to environmental gradients in the field, it is important to bear in mind that the ecological behaviour of species may differ greatly from that expected on the basis of their physiological propensities. The ecological optimum of a species in relation to one or more environmental gradients may not co-incide with its physiological optimum (Ellenberg 1954; Mueller-Dombois and Ellenberg 1974; Austin 1982; though see Ernst 1979).

Whittaker (1951, 1956) described the ecological response curves of tree species along altitudinal and topographic moisture gradients in the Great Smoky Mountains as "rounded or bell-shaped" with "tapered tails" and suggested that they may be of binomial form. Binomial curves are unimodal, but may be skewed. He also recognised flat-topped (plateau) bimodal and shouldered forms, but considered these to be special modifications of the more usual unimodal type. Later, Gauch and Whittaker (1972a) asserted that most species response curves approached the normal or Gaussian form. Their choice of the Gaussian function as a descriptor of response curve shape may have been largely one of convenience, for the purpose of modelling. Several other functions can

give rise to unimodal, bell-shaped curves (cf. Austin 1976a) and no rigorous statistical analysis was apparently performed in order to determine whether or not the Gaussian function was indeed the most appropriate of the possible alternatives. Recently, some authors appear to have accepted the Gaussian response curve as an observational fact (e.g. Westman 1980), despite the admission by Whittaker himself (see Austin 1976a) that asymmetrical and multimodal forms may be more common among his results than the symmetrical, unimodal (Gaussian) type. Werger, Louppen and Eppink (1983) found that only 31% of the species occurring along a soil nutrient gradient had response curves which could be adequately fitted by a Gaussian regression.

It has been pointed out (Greig-Smith 1980) that there is no theoretical reason to expect the relationship between species abundance and an environmental gradient to be Gaussian. The Gaussian function arises in statistical theory as the expected shape of the frequency distribution of a variable, when departures of values of the variable from some central or "expected" value may be attributed to a large number of independent factors, each of which has only a small effect. There is no clear analogy between this situation and the postulated role of the Gaussian function as the general form of the relationship between species performance and gradients. There is no reason to expect a symmetrical ecological response curve, since different processes are likely to limit a species' performance on opposite sides of its optimum. Thus, even without interspecific interactions, skewed curves might be anticipated.

Austin (1976a, 1980) has stressed the need for an adequate model

of vegetational response to environmental gradients before further significant improvements in the methodology of indirect gradient analysis are possible. A suitable model will have to take into account both the form of the ecological response curves of individual species and systematic variations in community characteristics (e.g. total abundance, alpha diversity, dominance) along gradients. At present, the clearest statement of such a model appears to be that of Gauch and Whittaker (1972a, 1976), but their model is deficient in several respects. Austin (1980) makes a plea for many more direct gradient analyses, based on appropriate methods of sampling, in order to provide the necessary observational evidence for the formulation of a general model. The present study attempts to make some contribution in this regard.

The major results of this study which are relevant to the formulation of vegetation-gradient models may be summarised as follows:

(1) The ecological response surfaces of species to the altitude X drainage ecoplane appeared to be predominantly unimodal (80%), although bimodal and multimodal types were by no means rare (20%). Of the unimodal species, somewhat more than half had response surfaces which were approximately symmetrical, the remainder being skewed or shouldered.

(2) Some differences were noted in the proportional representation of different response curve shapes between growth-forms. For example, all tree species had unimodal distributions.

(3) For unimodal species, the modes of the response surfaces were randomly scattered over the ecoplane defined by altitude and drainage. This applied to the total set of species, and to the

various growth-form groups delimited. There was no indication that the modes of "major" species were evenly spaced.

(4) The frequency distribution of mean cover at the mode agreed reasonably well with lograndom expectation for the full set of unimodal species. However, when species were partitioned into woody and non-woody sub-sets, only the latter had a lograndom distribution. For woody species the frequency distribution did not fit lograndom or lognormal hypotheses.

(5) Total cover (the sum of the cover values for all species in a sample) displayed a well defined pattern of variation in relation to altitude. The trend surface for this community characteristic was broadly unimodal, although not simply bell-shaped.

(6) Alpha diversity (mean number of vascular plant species per $100m^2$ sample) displayed a reasonably complex trend surface in relation to altitude and drainage. The pattern of alpha diversity was clarified when species were divided into growth-form groups. For each of the best represented growth-form groups, the trend surface for alpha diversity was unimodal. The complex trend surface for total alpha diversity could thus be regarded as the result of the overlap of the simpler, unimodal trend surfaces for each growth form.

(7) Percentage dominance and Simpson's index, both of which measure the degree to which cover is concentrated into a few major or dominant species within a sample, did not display any systematic trends over the altitude X drainage ecoplane.

(8) Mean height of the tallest stratum had a unimodal trend surface, with the mode on well drained to excessively drained sites at the lowest altitudes studied. Decrease in mean height with increasing

altitude appeared to be gradual, with no sharp transition at the position of the tree limit for Eucalyptus coccifera (c. 1220m). However the decline in canopy height with deteriorating drainage conditions below 1100m showed a relatively sharp transition from moderately drained to poorly drained conditions.

(9) The probability of occurrence of species also showed systematic trends along the altitudinal and drainage gradients. For most of those species for which modelling was attempted, the response surface for probability of occurrence was fitted adequately by a unimodal, bell-shaped function.

(10) Quantitative "noise" levels in this data set were relatively high. This is reflected in the generally low percentage of variance accounted for by the fitted response surfaces for percentage cover of 18 selected species.

These results were taken into account when designing the vegetation-gradient models used in the comparative evaluation of ordination methods reported in Part 1 of this thesis. Points (1), (4) and (6) suggest that vegetation-gradient models should make allowance for possible differences in behaviour of different growth-form groups; this possibility was not explored in the current modelling approach.

Most published applications of direct gradient analysis have dealt with forest communities (e.g. Whittaker 1956, 1960; Whittaker and Niering 1965; Loucks 1962; Beschel and Weber 1962; Mark and Sanderson 1962; Mark 1963; Westman 1975; Ashton 1976; Peet 1981) and some have investigated tree-less communities such as grassland and prairie (e.g. Ayyad and Dix 1964; Perring 1959, 1960). However, there appear to be

few examples of the application of direct gradient analysis to a vegetation pattern which includes elements of more than one major structural formation (Bray 1956; Wells 1960; Langenheim 1962; Brown and Podger 1982). This may have fostered the belief, referred to by McIntosh (1967), that the compositional continua demonstrated by gradient analysis occur only within the boundaries of the major physiognomically and structurally defined formations, with relatively sharp compositional discontinuities occurring between the formations.

The vegetation pattern analysed in the present study encompasses a variety of structural types, including forest, heath, and sedgeland. The results clearly demonstrate the lack of well-marked compositional discontinuities between the subalpine open-forest/woodland communities and alpine and subalpine open-heath communities on the Mt. Field Plateau. The subalpine forests, which are dominated by Eucalyptus coccifera and/or E. subcrenulata, would be considered part of the Sclerophyll Forest formation, while the alpine open-heaths are referrable to the Austral-montane formation (Jackson 1965). The subalpine tree-less vegetation would probably be regarded as an "edaphic disclimax" within the Sclerophyll Forest formation. An examination of the response surfaces of the 111 species for which adequate data was available, failed to reveal distinct groups of species with distributional limits co-inciding with the boundaries of these structural formations. Numerous examples could be cited of species whose distributional ranges transgress the formation boundaries. The individualistic nature of species distributions thus results in compositional continuity between the structural/physiognomic formations.

The concept of compositional continuity should not be confused

with the question of the existence or otherwise of sharp boundaries between plant communities on the ground. It is recognised, for example, that the transition from subalpine open-forest or woodland to subalpine open-heath may be extremely abrupt. However, such sharp boundaries are associated with sudden transitions from well drained or excessively drained conditions (class 4-5) to poorly drained or waterlogged conditions (class 1-2). Discontinuities in vegetational composition are expected when environmental conditions change abruptly. However, the fact that compositional variation along the drainage gradient is essentially continuous can be appreciated by noting that the vegetation of moderately drained sites at similar altitudes to such boundary situations is compositionally intermediate between the "community-types" occurring on either side of the environmental discontinuity. Confusion between continuity "on the ground" and compositional continuity in the abstract was relatively widespread in the ecological literature of the 1950's and 1960's.

A basic uncertainty underlies all direct gradient analyses, namely that the gradients chosen for study may not be the only important gradients influencing the vegetation. The results of an indirect gradient analysis (using an appropriate method) should help to indicate whether or not any important underlying gradients have been ignored in an associated direct gradient analysis. The following chapter explores the application of indirect gradient analysis methods to the vegetation pattern of the Mt. Field Plateau.

CHAPTER 9 : INDIRECT GRADIENT ANALYSIS

9.1 Introduction

Indirect gradient analysis and direct gradient analysis are complementary research strategies, aimed at understanding the continuous aspects of vegetational variation and underlying gradient relationships (Whittaker 1967). Direct gradient analysis is conceptually the simpler approach, and it is also the more fundamental. It is only by careful observation of the manner in which the abundances of species and the characteristics of communities vary along directly measured gradients that the most appropriate methodology for indirect gradient analysis can be devised (cf. Austin 1980). However, it is often difficult to find a reliable index of sample position along a recognised gradient (e.g. the drainage gradient at Mt. Field). There is a danger that the use of a crude index will intermingle samples which occupy different positions on the gradient, hence blurring or distorting the observed trends. In indirect gradient analysis, the compositional similarities of samples from similar positions on underlying gradients should ensure that they remain relatively close together in the ordination. Where environmental measurements are crude or unreliable, the compositional axes derived by indirect gradient analysis may therefore provide a more satisfactory representation of the positions of samples along the underlying gradients than could be obtained by direct ordination.

Another major difficulty with direct gradient analysis is that there is no guarantee that the environmental gradients chosen for study are indeed the sole, or at least the major gradients influencing the vegetation. Indirect gradient analysis helps to guard against this

possibility, since the existence of other gradients should be signalled by the extraction of unanticipated compositional trends. Vegetational ordinations may therefore act as a powerful stimulus to the generation of hypotheses about vegetation-environment relationships.

Direct gradient analysis (Chapter 8) has suggested that the subalpine and alpine vegetation of the Mt. Field Plateau forms a compositional continuum, in relation to two major environmental complex-gradients, related to altitude and drainage. However, the possibility that other, unrecognised gradients may underlie some of the compositional variation can not be ruled out. The application of indirect gradient analysis to the Mt. Field data was therefore expected to provide answers to the following questions:

(1) Are there two main compositional trends in the vegetation data, which can be related to the perceived altitudinal and drainage complex-gradients?

(2) If so, to what extent did the use of relatively crude indices of gradient position in the direct gradient analysis blur or distort these trends?

(3) Are there any other compositional trends, which can be attributed to other underlying environmental (or successional) gradients?

In addition, the present study examined a number of methodological problems. These were:

(1) The relative success of ordinations based on qualitative (i.e. presence-absence) data, cover estimates (i.e. midpoints of cover classes) and integer cover class scores.

(2) The robustness of ordinations to likely errors in the assignment of cover scores.

(3) The effect of quadrat size on ordination results.

(4) The relative performance of different ordination techniques. In view of the results of the simulation study, reported in Part 1 of this thesis, the success of LNMDS, relative to DCA, was of major interest.

9.2 Methods

9.2.1 Total Data Set (Individual Quadrats)

From the full set of 438 quadrats collected (section 7.1), 14 quadrats with heterogeneous drainage conditions and 20 burnt by wild-fires in the 1960's were excluded from the present analyses. The resulting data matrix included records for 205 species, although some of these were of very infrequent occurrence. To reduce the number of species to a manageable level, species occurring in less than five quadrats were deleted. In addition, members of the Orchidaceae were deleted, because of the fragmentary and unreliable nature of their records. Subsequenty, it was necessary to exclude six quadrats whose dominant species (i.e. species of highest cover) had previously been excluded due to infrequent occurrence. The final data matrix contained data for 139 species in 398, $100m^2$ quadrats. This matrix is henceforth referred to as the "total data set".

Although Local Non-metric Multidimensional Scaling (LNMDS) performed better than Detrended Correspondence Analysis (DCA) in the present simulation study (Part 1 of this thesis), limitations of the available software and considerations of computational cost made the application of LNMDS impractical with 398 quadrats. DCA was therefore

adopted as a primary approach for indirect gradient analysis. The total data set was subjected to several ordinations by DCA, using the program DECORANA (Hill 1979a). In view of the large number of quadrats, the number of segments for detrending in DECORANA was set at 40, rather than the default value of 26. Other options were set at the recommended values. Details of the data used in the DCA ordinations were as follows:

(1) The original integer cover class scores. The use of these scores amounts to a transformation of percentage cover which down-weights the effects of dominant species (see Table 7.1).

(2) Percentage cover (the midpoints of the cover classes, as shown in Table 7.1).

(3) Presence-absence records only.

(4) Integer cover class scores, with 10% of the values in the matrix altered at random to the next higher or lower value. When introducing these errors, values of 1 were not reduced to 0, since the presence of a species was considered indisputable. Similarly, values of 6, the highest class, could only be reduced.

(5) Integer cover class scores, with 20% of the values randomly perturbed as in (4).

In order to investigate the effect of quadrat size, a total data matrix was also prepared using the cover class data for the $10m^2$ sub-quadrats (see section 7.1). It was necessary to exclude nine of the quadrats included in the $100m^2$ total data set, because they contained less than two species. These quadrats were all located on boulderfields and screes with sparse vegetation cover, mostly at altitudes greater than 1300m. The final data matrix contained cover class data for 122

species in 389, $10m^2$ quadrats. This data set was ordinated by DCA, and the results were compared with the DCA ordination of the $100m^2$ quadrats.

9.2.2 Total Compound Data Set (Cluster Centroids)

Because the number of quadrats in the total data set was too large for LNMDS and PCoA, a compound data set was produced. The total data set was subjected to an agglomerative, hierarchical classification, using the Minimum Sum-of-Squares fusion criterion of Ward (1963; see also Orloci, 1967). This strategy was chosen because its "space dilating" property (Williams, Clifford and Lance 1971) tends to result in the equitable dissection of continuous data structures. The present aim was not to search for "natural" clusters, but merely to subdivide the total set of quadrats into a manageable number of groups, which effectively covered full range of compositional variation. The classification was performed on a matrix of squared chord distances (Orloci 1967) between each pair of quadrats. The distances were computed from the integer cover class scores, rather than midpoint cover values. The program package CLUSTAN (Wishart 1978) was used to perform the computations. The classification was arbitrarily intercepted at the 60 group level, 60 samples being considered a reasonable number for LNMDS. The groups at this level contained between two and 21 quadrats. From each group, a compound-quadrat was formed, by averaging the cover class scores for each species over the quadrats included in that group. The resulting data matrix contained average cover class scores for 139 species in 60 compound-quadrats. It will henceforth be referred to as the total compound data set.

The total compound data set was ordinated by the following

methods:

(1) DCA, using the program DECORANA with default option settings. Two DCA ordinations were performed. The first used the average cover class scores, while the second transformed all non-zero values to unity, and hence operated on only the presence or absence of species in the compound-quadrats.

(2) Local Non-metric Multidimensional Scaling (LNMDS), using the program KYST (Kruskal, Young and Seery 1973). LNMDS was applied in the same form used in Part 1 of this thesis (see section 2.3). Ordinations were performed in both two and three dimensions, operating on a percentage similarity matrix and using the quantitative DCA ordination (axes 1, 2 and 4) as an initial configuration. A two-dimensional LNMDS was also performed using the Sorenson coefficient of community.

(3) Global Non-metric Multidimensional Scaling (GNMDS), also using the program KYST. GNMDS was performed in three dimensions, using compound-quadrat scores on axes 1,2 and 4 of the DCA solution as an initial configuration and operating on a matrix of percentage similarity coefficients.

(4) Principal Components Analysis (PCA), using an original program, incorporating the eigenanalysis subroutine EIGRS (International Mathematical and Statistical Libraries, Inc. 1980). PCA ordinations were performed with each of the three data standardisations used in Part 1 of this thesis (section 2.3). These were: (a) unstandardised, centred by species (PCA-C), (b) centred by species and standardised by species standard deviation (PCA-CS) and (c) Bray-Curtis double standardisation followed by centring by species (PCA-BC).

(5) Principal Co-ordinates Analysis (PCoA), using another original program, incorporating the subroutine EIGRS. PCoA was performed on a matrix of percentage similarity coefficients.

9.2.3 Altitudinal Sub-sets

The total data set (398 quadrats) was subdivided, on the basis of altitude, into five sub-sets. The limits of the altitude classes were identical to those previously employed in the computation of beta diversities (section 8.2, Table 8.7). The numbers of quadrats in the resulting sub-sets were, in order of increasing altitude, 50, 115, 98, 116 and 19. In each sub-set, species occurring in less than three quadrats were deleted. The resulting matrices contained cover class data for 96, 107, 104, 86 and 36 species respectively. For convenience of discussion, the five sub-sets will be referred to below by the titles lower, middle and upper subalpine and lower and upper alpine.

Each sub-set was ordinated by DCA, using the program DECORANA with default option settings. Primary interest was centred upon the first axis of each ordination and its relationship to the drainage gradient. However, possible relationships between further axes and environmental (or other) gradients were also examined.

9.2.4 Interpretation and Comparison of Ordinations

The program DECORANA prints sorted lists, with species and quadrats ranked according to their scores on each ordination axis. These lists were found to be a useful initial guide to the interpretation of the compositional gradient associated with each axis. However it is difficult to gain an impression of the multidimensional relationships of species and quadrats purely from their rank order along individual axes. Furthermore, it is conceivable that the directions of compositional variation related to underlying gradients will be oblique to the ordination axes (e.g. Figure 4.1).

Consequently, a number of graphical aids to the inspection and interpretation of ordination results were developed. A program was designed to plot two-dimensional scatter diagrams, showing species or quadrat locations with respect to any pair of ordination axes. Other programs were designed to plot the values of individual species abundances, environmental variables or community characteristics (coded as integer class numbers, marker symbols or variable-sized glyphs) at the position of each quadrat on a selected pair of axes. These programs made extensive use of the subroutine library PLOT79 (Beebe 1979). A program was written to plot stereograms, following the method of Fraser and Kovats (1966). This allowed three-dimensional ordination configurations to be inspected. The program was adapted for an Hewlett-Packard 9825A desktop computer, from the BASIC program given by Orloci (1978a). The stereograms were plotted at a suitable size for viewing under a standard lense stereoscope.

Relationships between environmental variables and ordination axes,

or combinations of axes, were examined by means of least-squares multiple regression, using the interactive program TEDDYBEAR (Wilson 1979). The fitted models generally included scores on one or two ordination axes as predictors. Squared, cubic and product terms were included, if they resulted in a significant improvement in the percentage of variance explained. For ordinations of the compound-quadrats, mean values of environmental variables were computed in each of the 60 clusters, and regressions of these averages on the ordination axes were performed.

The degree of concordance between different ordinations of the same quadrats was assessed using the technique of Procrustean analysis (Schoneman and Carroll 1970), which has been described in section 2.2 (see Figure 2.3). The DCA ordination of the total data set (with cover class data) was adopted as a "standard", to which other ordinations of the total data set were compared. The method yields a goodness-of-fit measure, which is the RMS average of the displacement between each quadrat's location in the "standard" ordination and its position in the other ordination, after the latter has been brought into optimal agreement with the former. Its scale of measurement is that of the "standard" ordination, whose scaling is not altered during the fitting process. For ordinations of the total compound data set, the DCA ordination based on mean cover class values was used as a "standard".

By analogy with the simulation study reported in Part 1 of this thesis, it may be thought that the relative success of different ordinations of the Mt. Field data should be assessed by Procrustean fitting to the two-dimensional configuration defined by the altitudes

and drainage scores of each quadrat. However, in the case of the model coenoplanes, the co-ordinates of quadrats on the coenoplane axes represented precise indices of position along the simulated complex-gradients. In contrast, altitude, and especially drainage score, are only crude indices of position along the underlying complex-gradients. It is expected that a "successful" ordination will produce more accurate and continuous co-ordinates for quadrats along these gradients. Hence a perfect fit between ordinations configuration and the altitude v. drainage score configuration is not desired. There is also the problem of the relative scaling of the altitude and drainage gradients. The relative lengths of the model coenoplane axes were defined by their beta diversities. The models were constructed in such a manner that the beta diversity in the direction of the X axis was uniform at all points along the Y axis, and vice versa. Estimates of the beta diversity of the altitude and drainage gradients at Mt. Field are available (Table 8.7). However, they do not suggest a simple rectangular structure. For example, the beta diversity of the drainage gradient tends to decrease towards higher altitudes. The derivation of an appropriate scaling for altitude and drainage gradients, which is consistent with these beta diversities, is no simple matter. In view of these difficulties, the relative performance of ordination techniques was assessed primarily on the relative strength of the relationships between ordination axes and environmental variables (especially altitude and drainage score), as revealed by the regressions. The degree of curvilinear distortion of underlying gradients was investigated informally by examining the distributions of environmental variables on the ordinations, and the shape of the configurations with respect to three axes in the stereograms.

9.2.5 Analysis of Recently Burnt Alpine Sites

The 20 quadrats which fell on recently burnt sites have been excluded from all analyses thus far. This was done to avoid confounding the short term changes in vegetational composition and structure following fire with the patterns of variation along environmental gradients. Of the 20 burnt quadrats, five were subalpine and 15 were alpine (i.e. above the upper limit of Eucalyptus coccifera). Five subalpine quadrats was not regarded as an adequate number to enable an effective comparison of the post-fire communities of the subalpine and alpine tracts. The present analyses were therefore limited to the 15 alpine quadrats. Of these, nine were located along the south-western edge of the Mawson Plateau, and were burnt in 1961. The other six were on the north-eastern slope of the Rodway Range, above Tarn Shelf, which was subjected to a spot fire in 1966. The Mawson Plateau quadrats covered a reasonably wide range of drainage conditions (classes 2 to 5), but spanned an altitude range of only 1255 to 1270m. The Tarn Shelf quadrats varied in altitude from 1200 to 1300m and had all been placed in drainage class 3 or 4.

The major trends in compositional variation among the 15 alpine quadrats were investigated by subjecting cover class data for those 60 species which occurred in at least two of the quadrats to ordination by DCA. In order to investigate the relationships between pre- and post-fire vegetation, a "companion" quadrat was chosen for each burnt quadrat, from among the unburnt quadrats. Each unburnt quadrat was at a similar altitude to its associated burnt quadrat and had been placed in the same drainage class. Normally the paired burnt and unburnt quadrats

were adjacent on a sampling traverse. It was assumed that the pre-fire vegetation on each burnt quadrat was similar to that on the unburnt quadrat chosen as its companion. The cover class data for the 75 species occurring in at least two of the 30 paired quadrats was ordinated by DCA.

9.3 Results and Discussion

9.3.1 Major Compositional Trends and their Interpretation

DCA ordination of the total data set, using integer cover class data for 100m^2 quadrats, produced four axes with eigenvalues of 0.509, 0.377, 0.208 and 0.121. Inspection of the species scores on the first two axes suggested that axis 1 represented a compositional sequence related to the drainage gradient, while axis 2 described a compositional gradient related to altitude.

The distributions of cover values for selected species on the first two axes of the quadrat ordination are illustrated in Figure 9.1. In these plots, each quadrat in which the given species was present is represented as a square glyph, whose area is proportional to the percentage cover of the species. The 16 species illustrated were among the 18 for which modelling of probability of occurrence and cover was performed in section 8.3. Comparison of their distributions on the ordination with their observed and modelled responses to the altitudinal and drainage gradients (Appendix D), reinforces the notion that the two major compositional trends revealed by the ordination are closely related to the drainage and altitude gradients used in the direct gradient analysis.

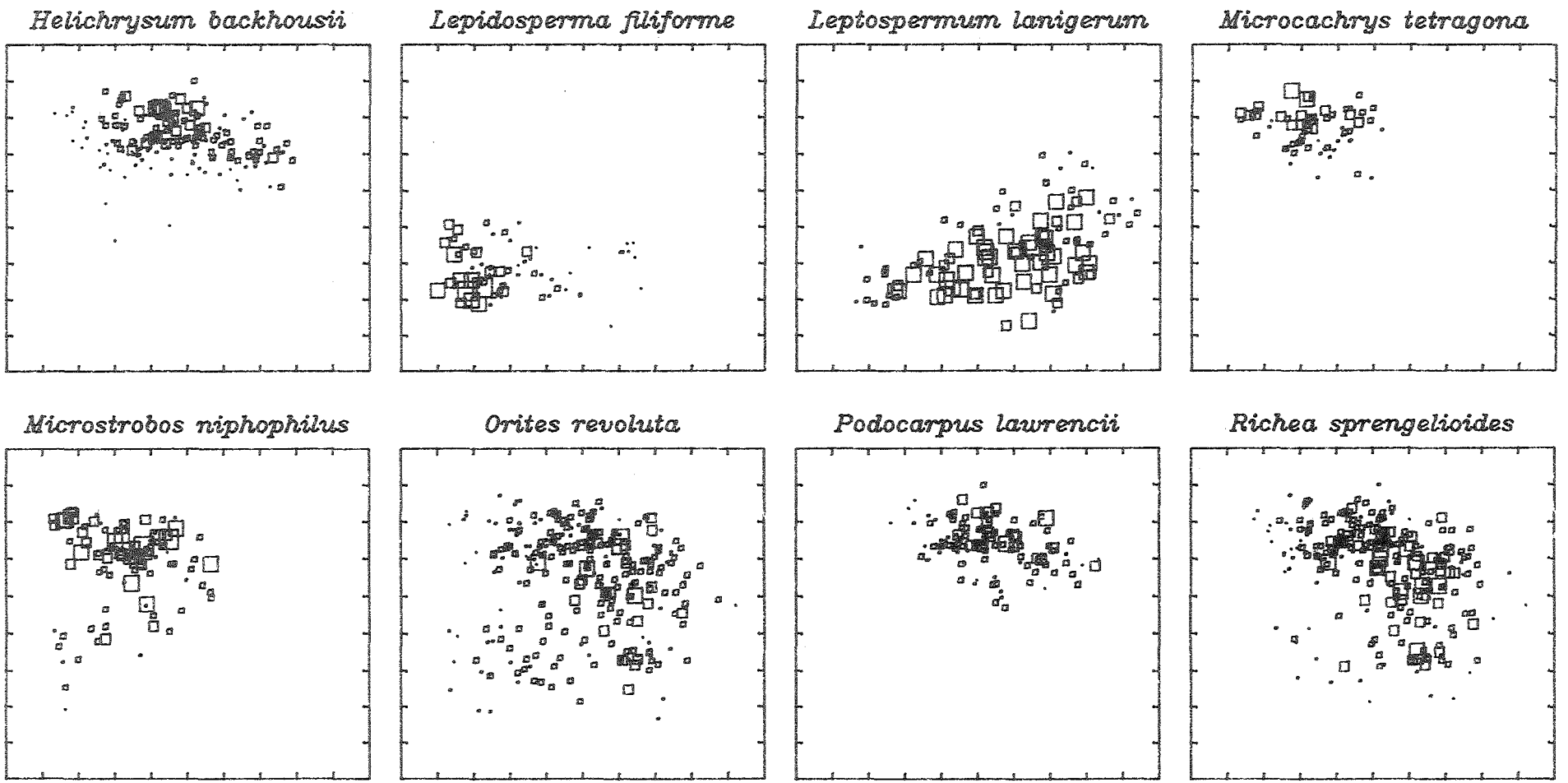


Figure 9.1 (continued)

The distribution of drainage scores on the first two axes of the quadrat ordination is shown in Figure 9.2. A marked gradation across the ordination is apparent. Samples with a particular drainage score tend to occur in relatively narrow zones or bands, but there are no discontinuities between the zones and the intermingling of quadrats with adjacent drainage scores often occurs. The band of quadrats with a drainage score of 1 is approximately perpendicular to the first ordination axis, but subsequent zones, corresponding to classes 2 to 5, are increasingly oblique to the first axis. Figure 9.3 shows the distribution of altitude with respect to the first two ordination axes. A strong relationship between altitude and the second axis is indicated. Although the bands of quadrats in the highest altitude classes are approximately perpendicular to the second axis, there is a tendency for the zones to become slightly curved with declining altitude. Both drainage and altitude therefore display marked trends in relation to the first two ordination axes. These trends are approximately at right angles to each other locally, but there is no simple, one-to-one correspondence between the ordination axes and the environmental indices. The plotting of other site characteristics on the first two axes of the ordination showed that slope and percentage rock cover, both of which are related to the drainage gradient, had patterns of variation similar to that displayed by drainage scores. Values of community characteristics such as total cover, height of tallest stratum and alpha diversity (for all species and various growth-form groups) had distributions on the ordination consistent with the patterns observed in the direct analysis.

In Table 9.1, the results of multiple regressions of drainage

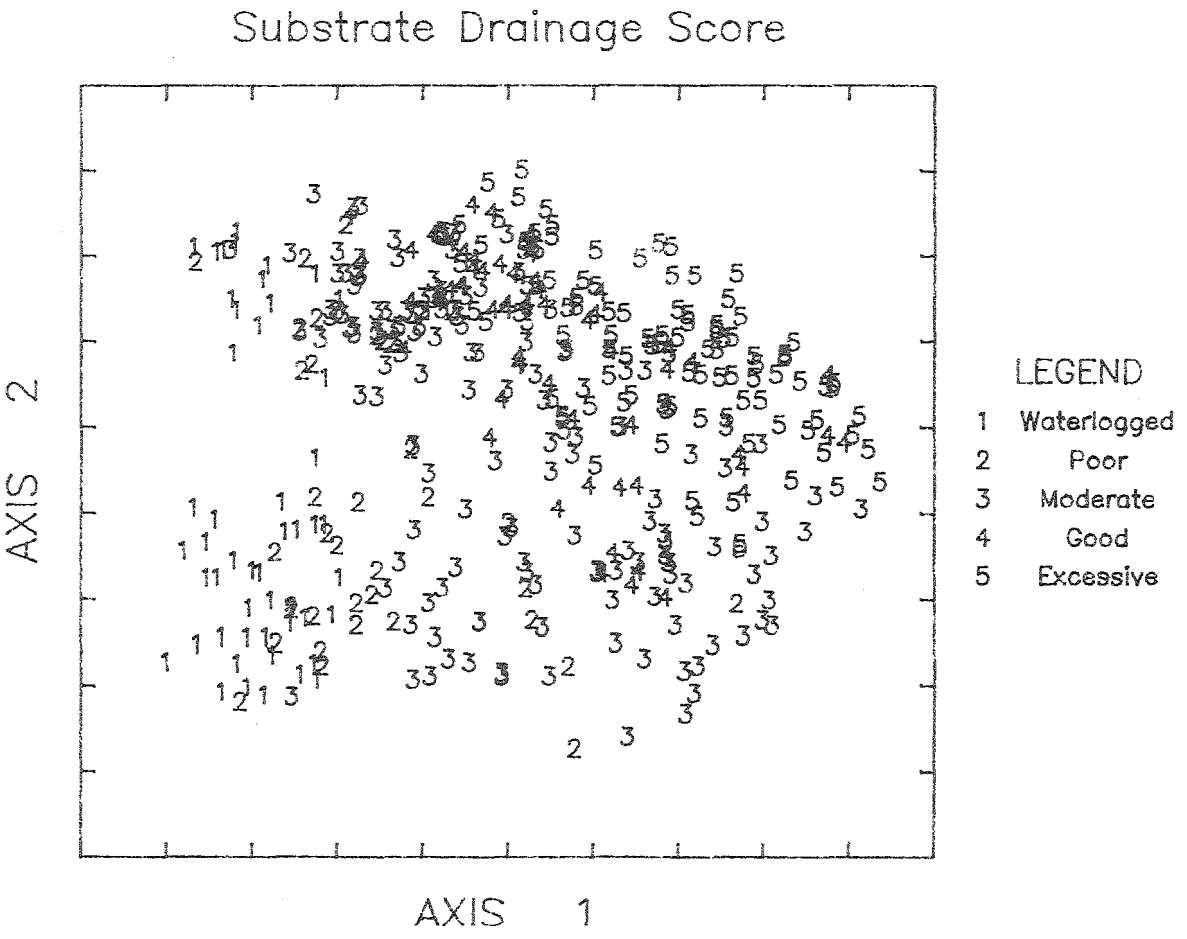


Figure 9.2 The distribution of drainage score within the configuration of quadrats defined by axes 1 and 2 of the DCA ordination of the total data set (cover class data).

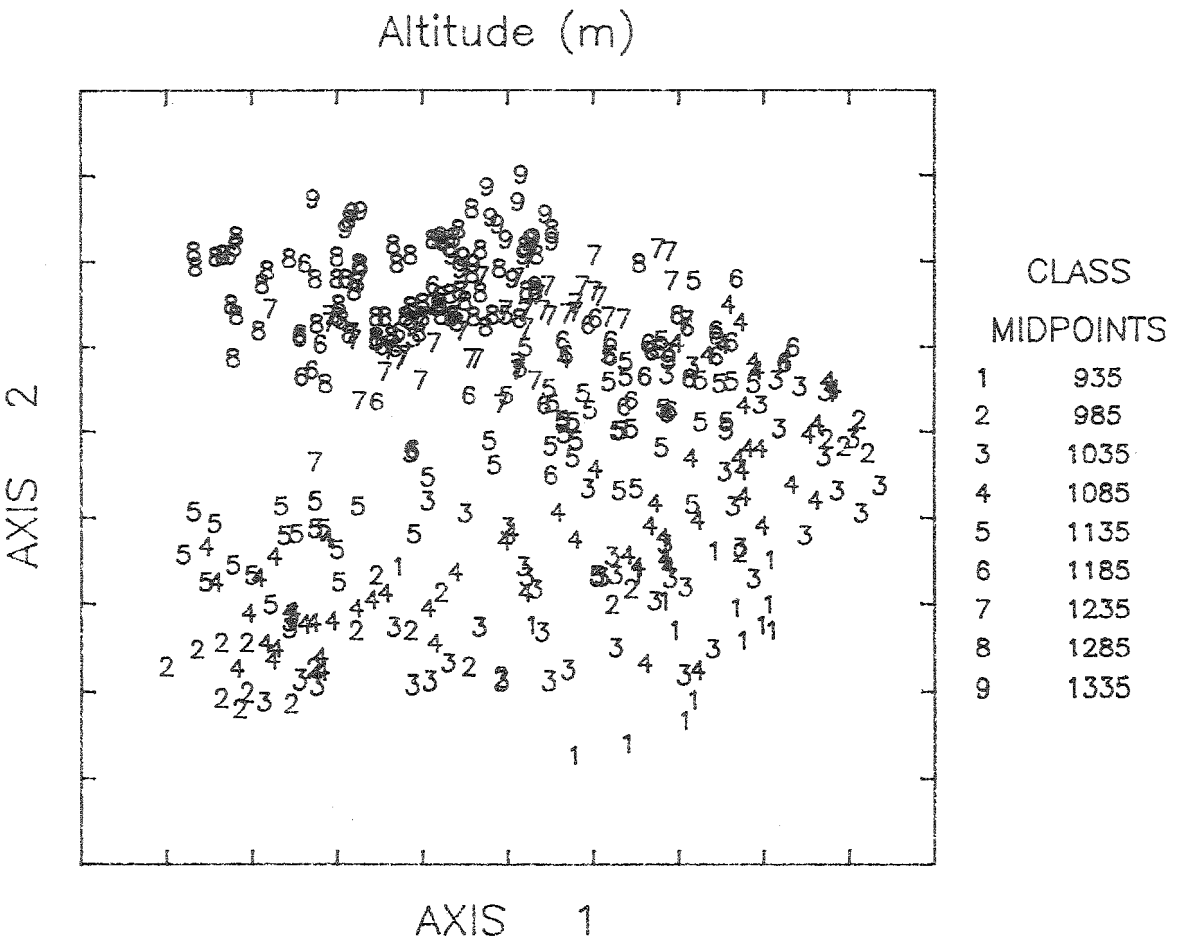


Figure 9.3 The distribution of altitude within the configuration of quadrats defined by axes 1 and 2 of the DCA ordination of the total data set (cover class data). For the sake of clarity, quadrat altitudes have been divided into nine classes.

Dependent Variable	DCA: 100 m^2 samples, cover class data				DCA: 100 m^2 samples, midpoint percentage cover data			
	Terms Required	r^2	F	p	Terms Required	r^2	F	p
Drainage score	$1, 1^2, 2, 2^2, 1x2$	78.3	287.0	<0.001	$1, 1^2, 2$	78.3	478.8	<0.001
Altitude	$1, 1^2, 2, 2^2$	85.4	581.8	<0.001	$1, 1^2, 2, 2^2, 1x2$	76.5	259.6	<0.001
Radiation	$4, 4^2, 4^3$	23.5	41.6	<0.001	No reasonable model			

Dependent Variable	DCA: 100 m^2 samples, presence-absence data				DCA: 10 m^2 samples, cover class data			
	Terms Required	r^2	F	p	Terms Required	r^2	F	p
Drainage score	$1, 1^2, 2, 2^2, 1x2$	76.3	256.2	<0.001	$1, 1^2, 1x2$	74.6	380.1	<0.001
Altitude	$1, 1^2, 2, 2^2$	85.6	592.9	<0.001	$1, 1^2, 2$	78.6	475.9	<0.001
Radiation	$4, 4^2, 4^3$	18.4	30.8	<0.001	$4, 4^2$	10.7	24.4	<0.001

Table 9.1 The results of multiple regressions of site characteristics on combinations of ordination axes, for DCA ordinations of the total data set, using various data types and sample areas. The r^2 values (percentage of variance explained) are computed from mean squares, rather than sums-of-squares. Approximate F ratio tests (regression mean square/residual mean square) for the significance of the entire regression, and their associated probabilities (p) are also given. For the three ordinations employing 100 m^2 samples, n=398. In the ordination based on 10 m^2 samples, n=389.

score and altitude on the first two ordination axes are given. The model for drainage required linear and squared terms for both axes, together with a product term. The adjusted r^2 (based on mean squares rather than sums of squares) was 78.3%. For altitude, a product term was not required, and the fitted model had an adjusted r^2 of 85.4%. These analyses confirm that quadrat scores on the first two axes are reasonably predictive of the environmental indices used for direct gradient analysis. The higher r^2 for altitude probably reflects the greater adequacy of altitude as an index of gradient position as compared with the crude, five step drainage scale.

The indirect gradient analysis therefore supports the underlying assumption of the direct gradient analysis: that the major compositional trends in the vegetation can be related to two complex gradients defined by altitude and drainage. The fan-like disposition of the altitudinal and drainage gradients in the ordination is a consequence of the decrease in beta diversity of the drainage gradient with increasing altitude (see Table 8.7). The greater compositional variation along the drainage gradient at the lower altitudes requires quadrats spanning the drainage gradient to be more widely dispersed in that part of the ordination. The relationship between beta diversity and the scaling of axes in DCA will be discussed in some detail later.

The third and fourth axes of the DCA ordination were examined for relationships with other environmental or successional gradients. Unfortunately, the third axis was found to be a spurious distortion axis. When plotted in the three-dimensional space defined by the first three axes, quadrats were scattered about a saddle-shaped surface. This

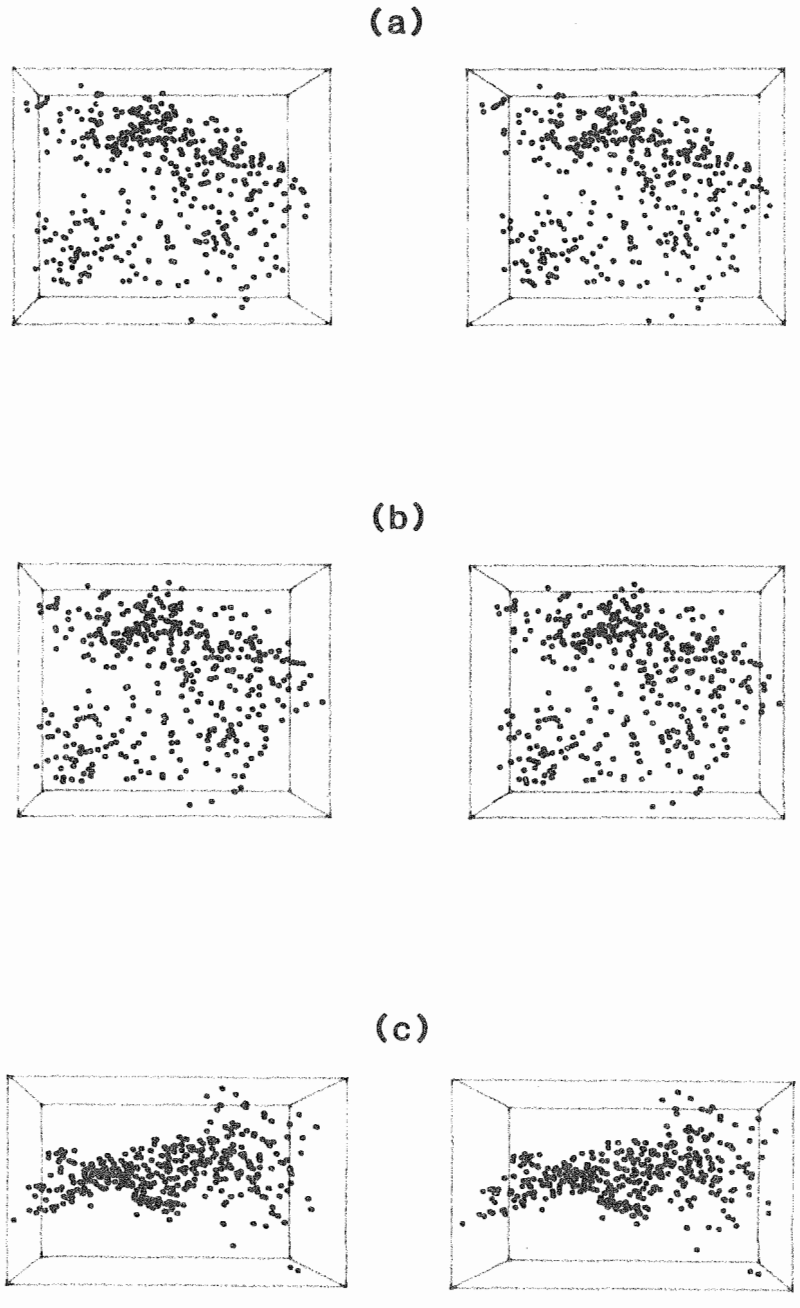


Figure 9.4 Stereograms showing the positions of quadrats with respect to selected sets of three axes in the DCA ordination of the total data set (cover class data). The identities of the X (horizontal), Y (vertical) and Z (normal to the paper) axes in the diagrams are as follows: (a) X=1, Y=2, Z=3; (b) X=1, Y=2, Z=4; (c) X=1, Y=4, Z=2.

is clearly visible in the stereogram presented as Figure 9.4a. Scores on the third axis are thus related to a combination of those on the first two axes by a curvilinear function. Hill and Gauch (1980) anticipated that such spurious "interaction" axes may arise in DCA, despite detrending. The detrending of third and subsequent axes is performed separately with respect to each previously extracted axis, but the possibility of strong curvilinear relationships with some combination of previous axes still remains. Gauch, Whittaker and Singer (1981) observed some examples of this phenomenon in ordinations of simulated vegetation data with three and four underlying dimensions. Hill and Gauch (1980) noted that the eigenvalues associated with such spurious axes were generally small in comparison to those of axes reflecting variation along real underlying gradients. In the present example the eigenvalue of the spurious axis (0.207) is relatively large in comparison to the eigenvalues of the first two, "real" axes (0.509, 0.377). Two-dimensional plots showing quadrat positions on axes 1 v. 3 and 2 v. 3 would suggest that the third axis bears no systematic relationship to either of the first two axes. It was only the examination of the stereogram (Figure 9.4a) which revealed the spurious nature of the third axis. A degree of caution is therefore recommended in attempting to interpret third and subsequent axes of DCA ordinations produced by the program DECORANA.

Examination of stereograms showing quadrat locations with respect to axes 1,2 and 4 (Figure 9.4b,c) indicated that the fourth axis was at least partially independent of the first two axes. The variation in scores on the fourth axis is greatest among quadrats located towards the upper extreme of the first axis. These are mostly quadrats with

drainage scores of 3 to 5 and altitudes less that 1200m (see Figures 9.2 and 9.3). The distributions of cover values for 8 selected species, on the two-dimensional quadrat ordination defined by axes 1 and 4, are shown in Figure 9.5. The species chosen for illustration are among those with extreme scores on the fourth axis. They are mostly species of relatively low frequency in the data set. Most of the "major" species, whose distributions on the first two axes were shown in Figure 9.1, do not display systematic trends in cover or frequency of occurrence along the fourth axis.

Species such as Nothofagus cunninghamii, Eucryphia milliganii, Orites diversifolia, Richea pandanifolia and Trochocarpa cunninghamii, whose occurrences tend to be concentrated towards the lower end of axis 4 (Figure 9.5), are regarded by Jarman and Brown (1983) as temperate rainforest species. They are all apparently capable of regeneration beneath a rainforest canopy, without the intervention of fire or other catastrophic events. The five quadrats with the lowest scores on axis 4 carry a low closed-forest of Nothofagus cunninghamii, Eucryphia milliganii, Atherosperma moschatum and the conifers Phyllocladus asplenifolius, Athrotaxis selaginoides and A. cupressoides. An emergent stratum Eucalyptus subcrenulata is present, but no eucalypt seedlings or saplings were observed. This forest is regarded as a subalpine variant of the "mixed forest" of Gilbert (1959). If a fire does not disturb the closed canopy of the rainforest tree species within the life span of the emergent eucalypts, the forest should revert to cool temperate rainforest (cf. Jackson 1968). Occurrences of mixed forest and cool temperate rainforest within the study area are rare and localised. Such forests were only observed at sites which are

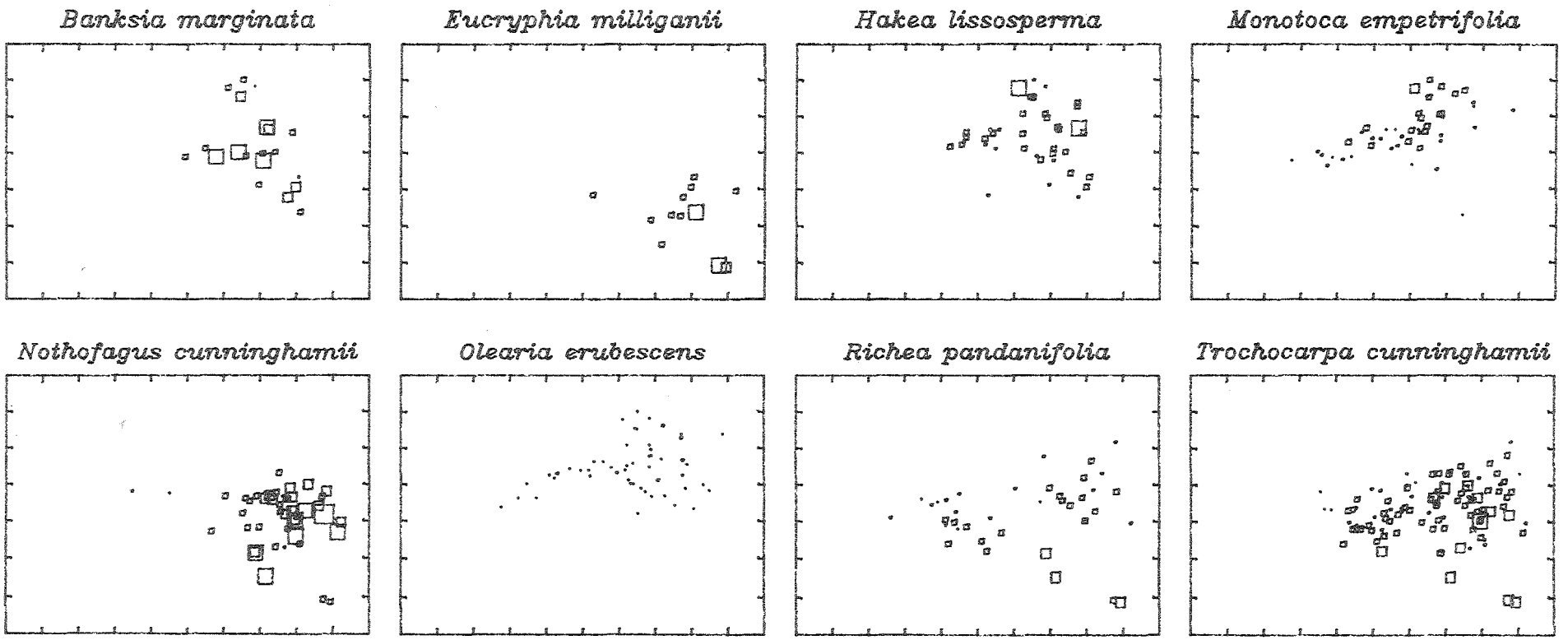


Figure 9.5 The distribution of percentage cover estimates for selected species within the configuration of quadrats defined by axes 1 and 4 of the DCA ordination of the total data set (cover class data). Each quadrat where the indicated species was present is marked by a square glyph, whose area is proportional to the estimated percentage cover of the species in that quadrat.

protected from fire by their topographic position and/or proximity to a large water body. The six quadrats with lowest scores on axis 4 are located on the south facing slope of Mt. Bridges (see Figure 7.1). They rarely receive direct sunlight, hence their estimated annual radiation figures are only 60 to 70% of those of level sites in the study area. The slope is also sheltered from the dry north to north-westerly winds in summer.

Species which typify the upper end of axis 4, such as Hakea lissosperma, Banksia marginata, Persoonia gunnii, Monotoca empetrifolia and Blandfordia punicea (Figure 9.5) are are mostly regarded as fire tolerant, and some may be dependent on fire for effective regeneration (W.D. Jackson, personal communication 1983). The quadrats with highest scores on axis 4 are located on well drained, north-west to north-east facing slopes or on glacial moraines, east of Lake Seal. They are well insolated and exposed to drying summer winds. The vegetation on such sites would have a high probability of being burnt in any major wild-fires which occurred in the region.

It is postulated that the compositional gradient represented by axis 4 is related to an underlying gradient in firing history. The positions of quadrats along the gradient may reflect either the time elapsed since the most recent fire, or the long term frequency of fires on the site (cf. Jackson 1968; Brown and Podger 1982). In view of the absence of precise information on the age or fire history of the forests in the study area, this interpretation must be regarded as tentative.

Of the site characteristics recorded in the present study, only annual solar radiation had a significant relationship with the fourth

axis. A cubic regression of radiation on axis 4 had an adjusted r^2 of 23.5% (Table 9.1). However, an inspection of the scatter plot of radiation versus score on axis 4 suggested that the relationship was largely attributable to the low radiation values for the six quadrats with ordination scores at the lower extreme of the fourth axis. When these six quadrats were excluded from the regression, no significant relationship could be detected between radiation and the ordination axis. Low radiation levels would tend to reduce the probability of the vegetation and litter on a site becoming sufficiently dry to carry fire. The relationship between radiation and the compositional gradient represented by axis 4 is therefore considered to be indirect.

Unfortunately, the program DECORANA extracts only four ordination axes. Because the third axis in the present analysis was a spurious interaction axis, the number of useful axes was reduced to three. The possible existence of other, potentially interesting compositional trends in the total data set could not be investigated.

The present indirect gradient analysis has provided answers to the questions posed in the introduction (section 9.1). These may be summarised as follows:

(1) The two major compositional gradients recognised by the analysis are closely related to the altitudinal and drainage complex-gradients, previously used for direct gradient analysis.

(2) There is no indication that the use of crude indices of quadrat location, especially along the drainage gradient, led to a false appearance of vegetational continuity in the direct gradient analysis.

(3) A third compositional gradient was identified. This gradient

operates among subalpine forest communities on well drained sites. It is suggested that it may be related to firing history. This interpretation is based on the known ecological behaviour, with respect to fire, of species and genera typifying the extremes of the gradient, as observed elsewhere in Tasmania (Gilbert 1959; Jackson 1968).

9.3.2 The Effects of Data Type

The DCA ordination of the total data set, using presence-absence data, was extremely similar to the cover class ordination. The four axes had eigenvalues of 0.472, 0.355, 0.187 and 0.107. As with the cover class ordination, the first two axes described compositional variation related to drainage and altitude (Figure 9.6). The third axis was a spurious interaction axis, and the fourth axis described the same compositional gradient among subalpine forests on well drained sites, which was revealed in the cover class ordination. The results of multiple regressions of drainage score and altitude on polynomial functions of the first two axes are given in Table 9.1. The fitted models had adjusted r^2 values of 76.3% and 85.6% respectively. These values are very similar to the corresponding figures for the cover class ordination, indicating that the presence-absence ordination is about equally predictive of these environmental indices.

Procrustean fitting of the quadrat configuration defined by the first two axes of the presence-absence ordination to that produced by the cover class ordination gave an RMS displacement error (D2) of 16.6 units. The fit was also performed in three dimensions, using quadrat scores on axes 1,2 and 4. This gave a D3 value of 25.9 units. These

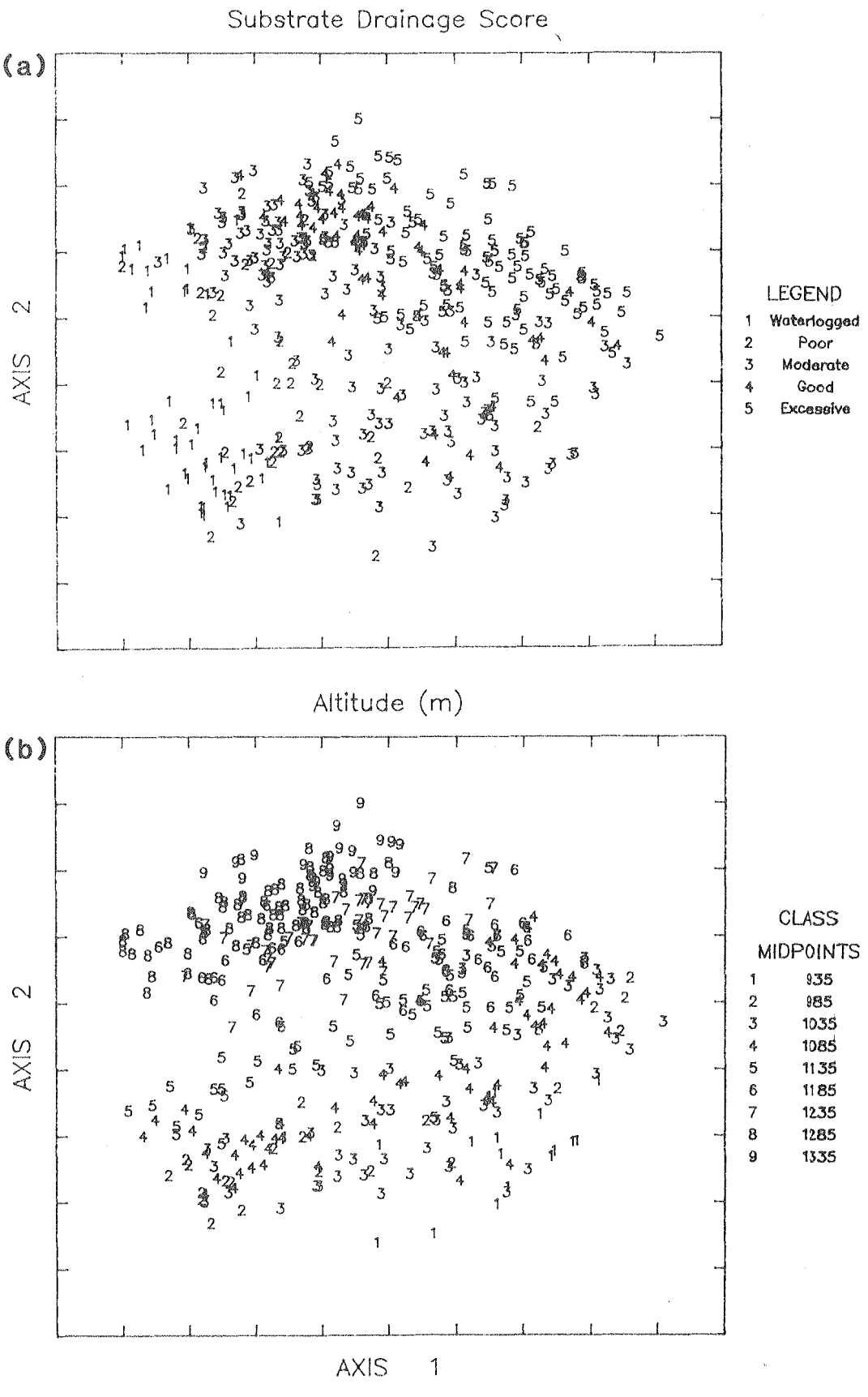


Figure 9.6 The distributions of (a) drainage score and (b) altitude (rounded to nine classes) within the configuration of quadrats defined by axes 1 and 2 of the DCA ordination of the total data set using presence-absence data.

displacement errors are expressed in the same units as the axes of the cover class ordination. The strong agreement between quadrat positions in the two ordinations, may be appreciated by noting that the tic marks along the axes in Figures 9.2 and 9.3 are 50 units apart.

These results indicate that, when the beta diversity of the underlying gradients is sufficiently high (at least 3 half-changes of the percentage similarity coefficient), indirect gradient analysis based on presence-absence data can be comparable in effectiveness to an analysis based on cover scores. It may seem anomalous that binary data can give rise to a relatively continuous estimate of gradient position. If species occurrences along a gradient were localised in adjacent blocks of quadrats, such that the species was present in all quadrats within the block and absent in all other quadrats, then there would exist regions of the gradient in which all quadrats had identical species lists. The precision with which an indirect gradient analysis operating on presence-absence data could specify the correct location of a given quadrat on the gradient would be limited by the width of such regions. However, it has been shown in the previous chapter (section 8.3) that species occurrences are not simply concentrated into blocks along the altitudinal and drainage gradients. For most of the species examined, probability of occurrence along the gradients was fitted adequately by a bell-shaped function. It seems likely that the smoothly tapering form of the relationship between probability of occurrence and gradients would allow relatively detailed information about gradient position to be "encoded" in qualitative data.

When planning the sampling strategies for an indirect gradient

analysis, the possibility that presence-absence data may suffice should be borne in mind. The collection of presence-absence data requires considerably less time and effort than most measures of species abundance. The resultant decrease in sampling time may allow more adequate numbers of quadrats to be collected. Hence the predictive value of the ordination analysis may be improved. Unless the purpose at hand calls for accurate measures of species abundance, the use of sophisticated sampling methods (e.g. point frames or line intercept sampling for percentage cover) may be unnecessary. These comments apply only to situations where beta diversities of the underlying gradients are greater than about 3 HC.

The DCA ordination of the total data set in which cover class scores were replaced by the midpoints of the cover classes (Table 7.1), produced four axes with eigenvalues of 0.673, 0.468, 0.299 and 0.244. As with the cover class and presence-absence ordination, the first two axes defined a two-dimensional compositional pattern (coenoplane) related to the altitudinal and drainage gradients (Figure 9.7). However, in comparison to the previous ordinations, the quadrat arrangement on the first two axes appeared distorted. In Figure 9.7b it will be observed that the bands of quadrats in each altitudinal belt are strongly curved. Furthermore, there is a "tongue" of quadrats protruding from the lower left of the configuration, in which quadrats with altitudes from classes 2 to 5 are superimposed. These quadrats are separated on the third ordination axis, as illustrated by the stereograms (Figure 9.8a,b). It thus appears that the altitude X drainage coenoplane has been severely warped in the cover ordination. The lower left corner of the coenoplane (corresponding to poorly drained

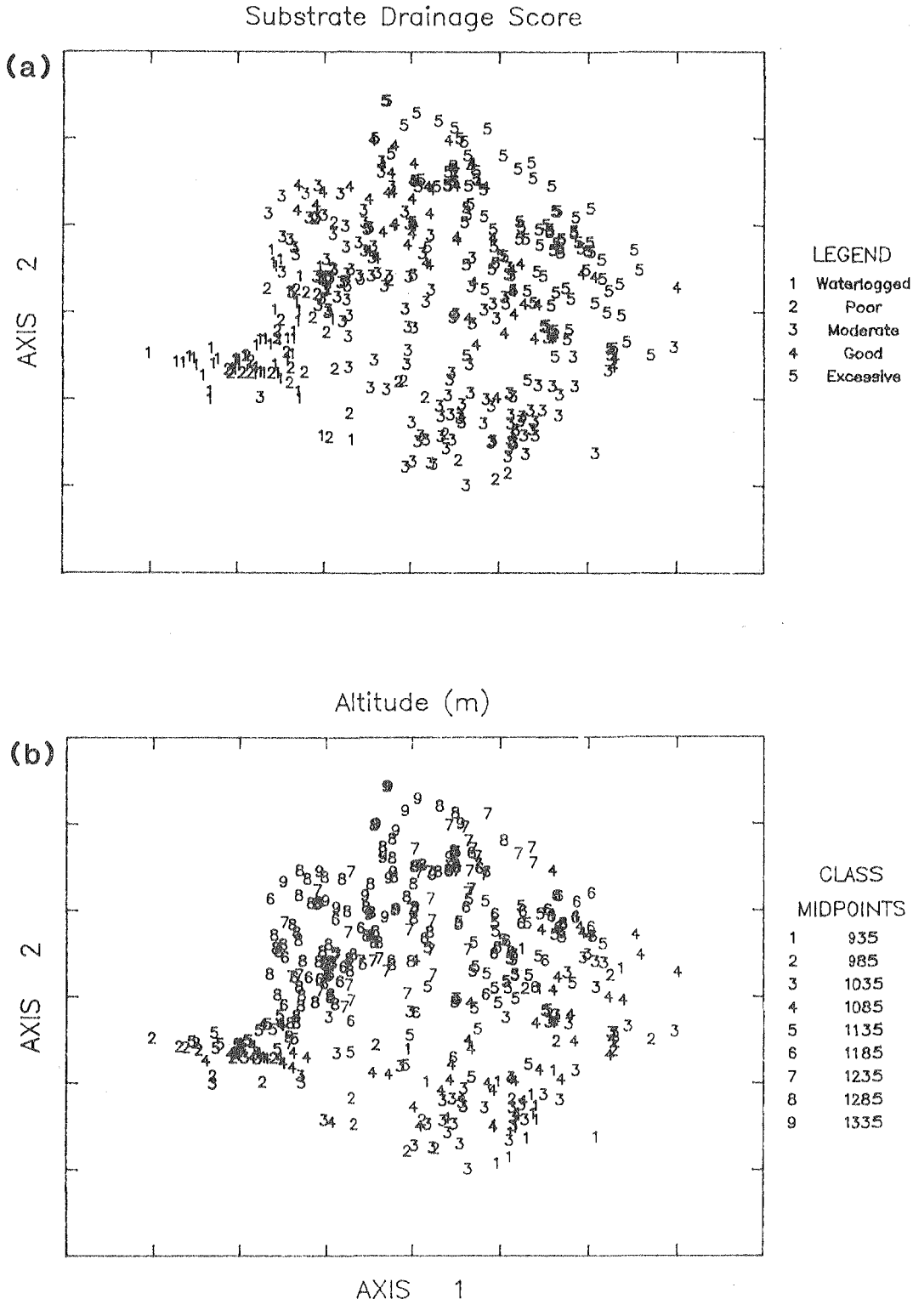


Figure 9.7 The distributions of (a) drainage score and (b) altitude (rounded to nine classes) within the configuration of quadrats defined by axes 1 and 2 of the DCA ordination of the total data set, using percentage cover data (i.e. midpoints of the cover classes).

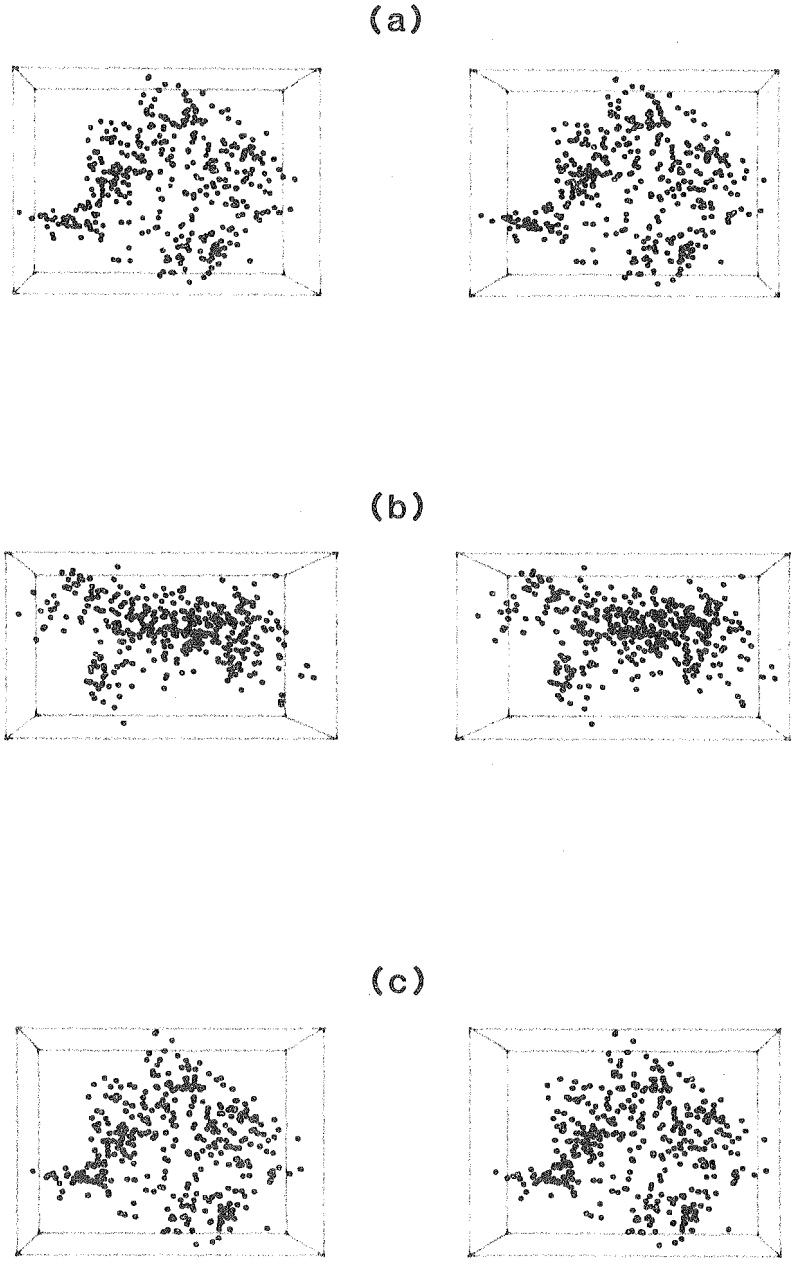


Figure 9.8 Stereograms showing the positions of quadrats with respect to selected sets of three axes in the DCA ordination of the total data set (midpoint percentage cover data). The identities of the X (horizontal), Y (vertical) and Z (normal to the paper) axes in the diagrams are as follows: (a) X=1, Y=2, Z=3; (b) X=1, Y=3, Z=2; (c) X=1, Y=2, Z=4.

to waterlogged, subalpine sites) has been twisted, so that the compositional variation in that region projects into a third dimension. This type of distortion is reminiscent of the DCA ordinations obtained with some of the coenoplane models in Part 1 of this thesis (e.g. Figure 4.4, upper left panel). The fact that the distortion appeared in the analysis of the Mt. Field data when midpoint cover values was used, but was not manifest in the cover class and presence-absence ordinations, suggests that it may be due to domination of the analysis by species which attain high cover values. The simulation approach used in Part 1 of this thesis could be applied to the investigation of this problem.

The results of multiple regressions of drainage score and altitude on polynomial functions of the first two axes of the cover ordination are presented in Table 9.1. The drainage model had an adjusted r^2 of 78.3%, which is comparable with the corresponding value for the cover class ordination. In view of the curvilinear distortion, this may seem surprising, however an examination of Figure 9.7a shows that the pattern of drainage scores is less affected by the distortion than the altitudinal pattern (Figure 9.7b). The r^2 for the altitude model was only 76.5%, this being markedly less than the corresponding figures for the cover class and presence-absence ordinations (Table 9.1).

Neither the third nor the fourth axis of the cover ordination represented an interpretable compositional gradient. As mentioned above, the third axis described some of the compositional variation in the severely twisted, lower left corner of the altitude by drainage coenoplane. The fourth axis was a totally spurious, interaction axis. Like the third axis in the cover class ordination, quadrat scores on the fourth axis were clustered around a saddle-shaped surface (Figure 9.8c).

The cover ordination thus failed to recover the third compositional gradient discussed in section 9.3.1 on its third or fourth axis.

A two-dimensional Procrustean fit of the cover ordination to the "standard" cover class ordination, using quadrat scores on the first two axes, gave an RMS displacement error (D2) of 45.5 units. This value is almost three times greater than the D2 value obtained when the presence-absence ordination was compared with the cover class ordination.

As a result of this analysis, it may be tentatively suggested that indirect gradient analysis based on species abundance data may be more effective if abundance data is transformed in a manner which down-weights the effects of species with large abundance values. Logarithmic or square root transformations of the abundance values prior to analysis should achieve this objective. More simply, an integer abundance scale with broader classes for the higher abundance values (such as the system used in the present study) may produce reasonable results.

The effects of various measures of species abundance or importance and presence-absence data on the results of numerical classifications have been examined by Smartt, Meacock and Lambert (1974, 1976). They suggested that quantitative measures which are sufficiently constrained to allow quantitative differences to operate within a framework of floristic (i.e. qualitative) diversity are likely to be most useful in ecological work. Approximate methods of recording, unless extremely crude, had less effect on classification results than a change to a different type of measure.

9.3.3 The Effect of Recording Errors

DCA ordinations of the total data set, using randomly perturbed cover class scores, produced results very similar to the ordination of the original cover class data. Ordinations of the perturbed data sets were compared with the original cover class ordination using Procrustean analysis. For the data set with 10% of the scores altered by one class, the D3 value (using axes 1,2 and 4) was only 6.6 units. The D3 value for the ordination of the data set with 20% of the cover scores randomly altered was 9.8 units. Even this value is less than the distances between many of the quadrats in the original ordination and their nearest neighbour. These results indicate that the indirect gradient analysis based on DCA of cover class data is robust to likely errors in assignment of cover scores to species.

9.3.4 The Effect of Sample Size

The DCA ordination of the total data set, using cover class scores for the $10m^2$ sub-quadrats, produced four axes with eigenvalues of 0.580, 0.422, 0.257 and 0.222. The distributions of drainage scores and altitude on the first two axes of the quadrat ordination are shown in Figure 9.9. The patterns are similar to those observed in the ordination of the cover class data for $100m^2$ quadrats (Figures 9.2 and 9.3). Multiple regressions of drainage score and altitude on polynomial functions of the first two axes (Table 9.1) had adjusted r^2 values of 74.6% and 78.6% respectively.

The primary reason for the ordination using $10m^2$ quadrats was to see whether continuity along the drainage gradient in the ordination of

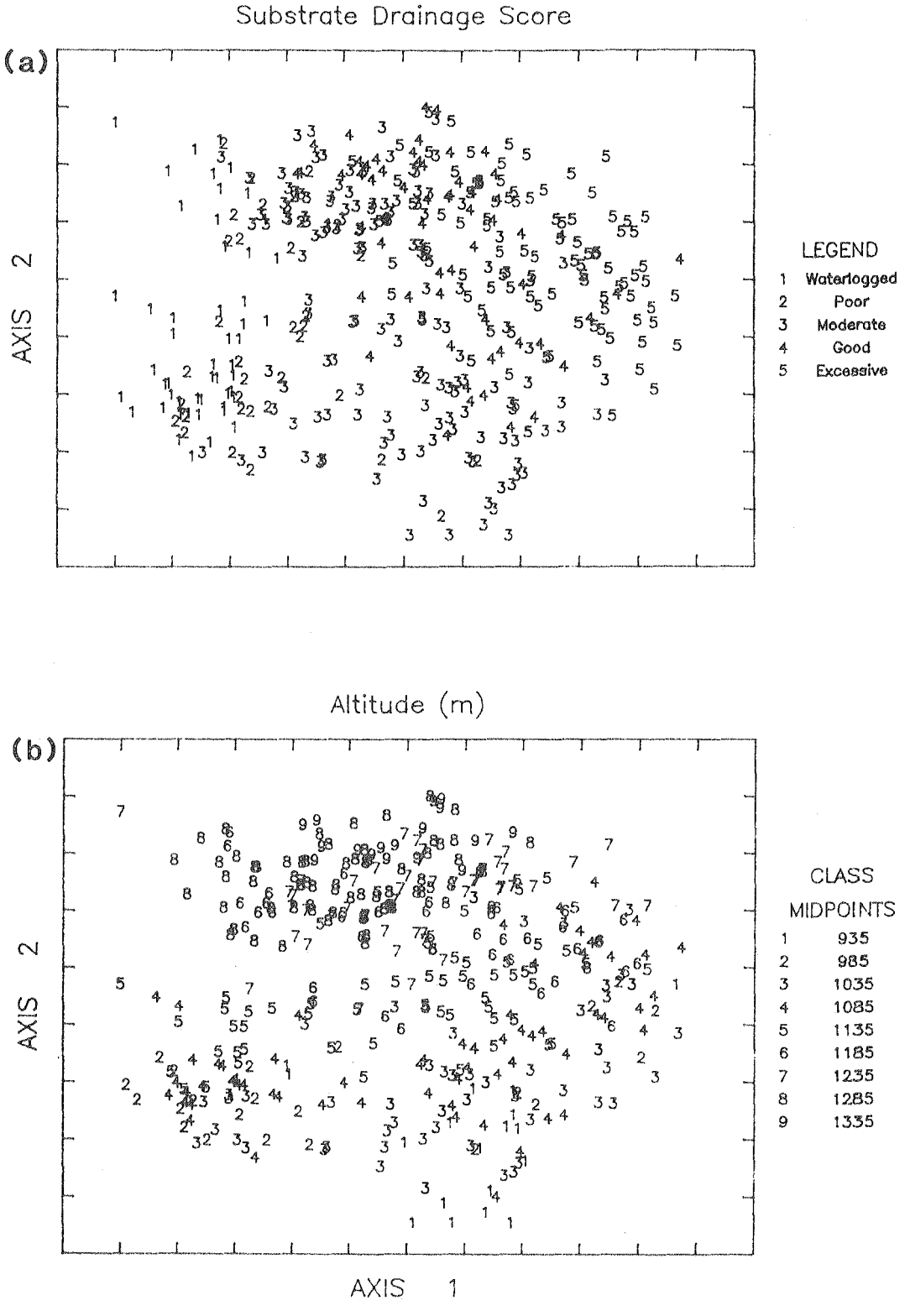


Figure 9.9 The distributions of (a) drainage score and (b) altitude (rounded to nine classes) within the configuration of quadrats defined by axes 1 and 2 of the DCA ordination of the total data set, using cover class data from the 10 m^2 sub-quadrats.

100m^2 quadrats was attributable to the inclusion of heterogeneous drainage conditions within the 100m^2 quadrats. There is no apparent tendency in the 10m^2 ordination for a greater degree of discontinuity or clustering along the compositional gradient related to drainage (Figure 9.9a). However, two quadrats at the extreme left of the ordination appear as relative outliers, because they possess high cover scores for two species of low frequency in the data set.

The third axis of the 10m^2 ordination was a spurious interaction axis of the same type obtained in the 100m^2 cover class ordination. The fourth axis described the compositional trend among forests on well drained, subalpine sites as was observed in the 100m^2 ordination. Procrustean fitting of the 10m^2 ordination to the 100m^2 ordination, using scores on axes 1,2 and 4, gave a D3 value of 42.8 units. The D2 value, based on axes 1 and 2 only, was 34.9 units. These statistics indicate that there is a reasonable degree of conformity between the two ordinations.

This analysis provides no evidence that the results of the direct gradient analysis or the previous indirect gradient analyses were biased by the use of 100m^2 quadrats. Compositional continuity is not an artifact due to the inclusion of heterogeneous edaphic conditions in the 100m^2 quadrats.

9.3.5 Analyses of Altitudinal Sub-sets

DCA ordinations of the five altitudinal sub-sets (see section 9.2.3) all produced a first axis which was related to the drainage gradient. The distribution of drainage scores on the first two axes of the ordinations for each of the subalpine sub-sets is illustrated in Figure 9.10. Similar plots for the two alpine sub-sets are given in Figure 9.11. There is an tendency for drainage scores to increase from left to right in each ordination. However, the bands of like drainage scores appear to be slightly oblique to the first axis in the ordinations of the lower and upper subalpine sub-sets (Figure 9.10a,c). Multiple regressions of drainage score, on polynomial functions of the first two axes, confirmed the oblique pattern for these two sub-sets (Table 9.2). The drainage models for the lower and upper subalpine sub-sets required simple linear terms for both axis 1 and axis 2. For the other three sub-sets, a simple linear regression on axis 1 proved to be adequate. The adjusted r^2 values for the three subalpine sub-sets and the lower alpine sub-set (Table 9.2) were comparable with the figure obtained for the DCA ordination of the total data set using cover class data (Table 9.1). The lower r^2 value for the upper alpine sub-set (54.7%) is attributable to the small number of quadrats in that altitude zone and the lack of waterlogged and poorly drained sites. The lack of such sites results in a markedly lower beta diversity along the drainage gradient (Table 8.7). Hence the ordination would be expected to be more severely affected by noise variation (see Chapter 3, section 3.2).

The primary compositional gradients identified by each of these ordinations could be used to derive indirect indices of quadrat position

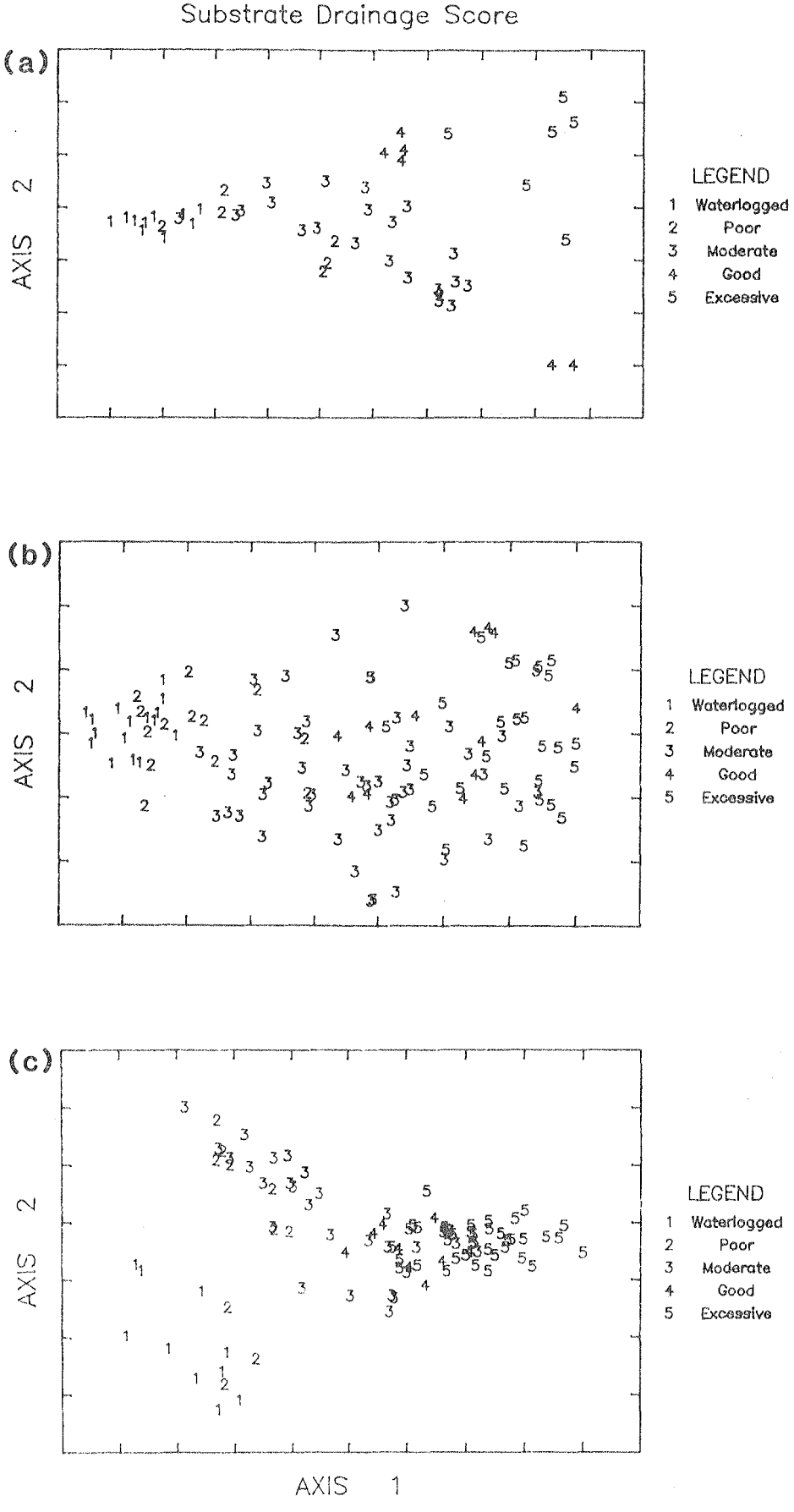


Figure 9.10 The distribution of drainage score within the configurations of quadrats defined by axes 1 and 2 of the DCA ordinations of (a) the lower subalpine sub-set, (b) the middle subalpine sub-set and (c) the upper subalpine sub-set. Each ordination was based on cover class data from 100 m^2 quadrats.

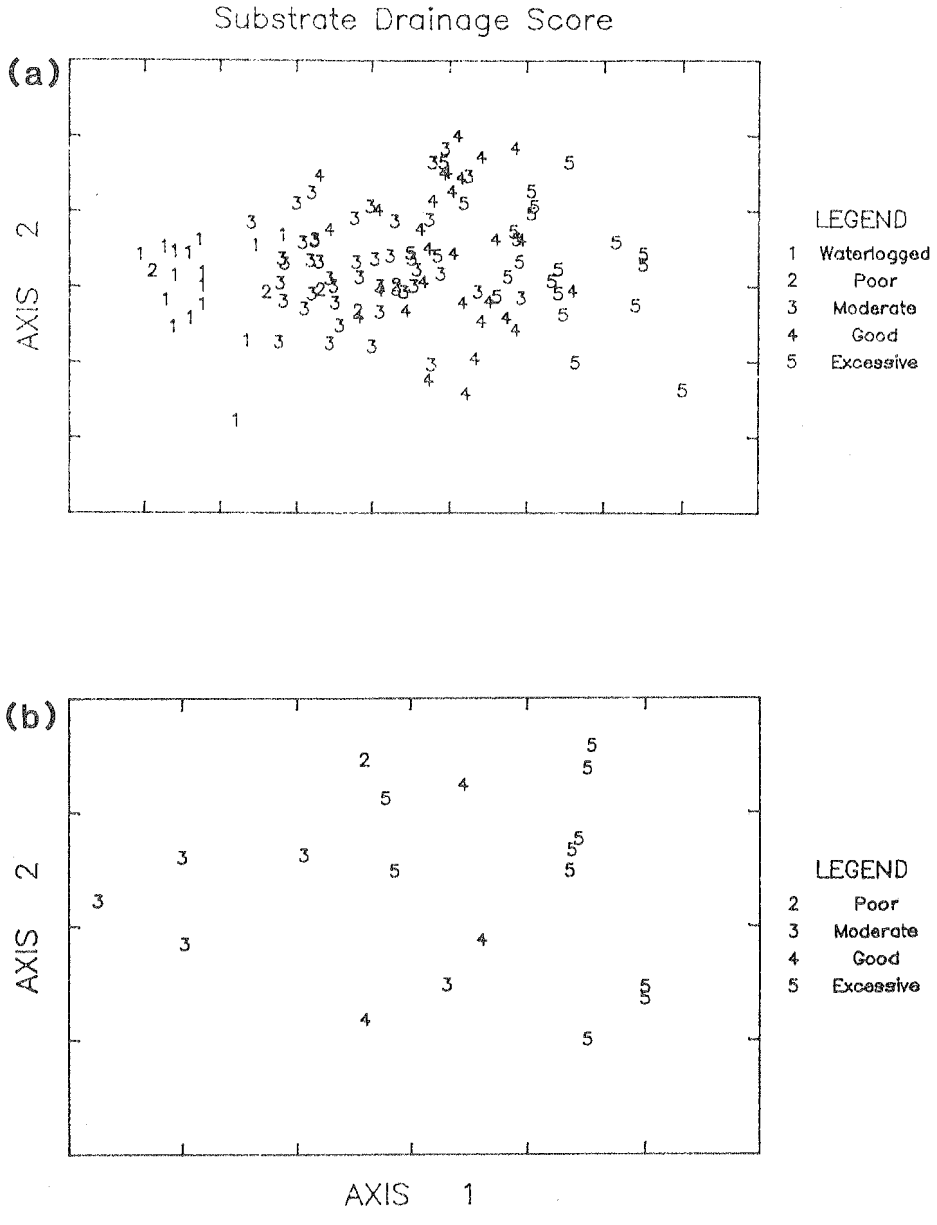


Figure 9.11 The distribution of drainage score within the configurations of quadrats defined by axes 1 and 2 of the DCA ordinations of (a) the lower alpine sub-set and (b) the upper alpine sub-set. Each ordination was based on cover class data from 100 m^2 quadrats.

Dependent Variable	Lower Subalpine (n=50)				Middle Subalpine (n=115)				Upper Subalpine (n=98)			
	Terms Required	r^2	F	p	Terms Required	r^2	F	p	Terms Required	r^2	F	p
Drainage score	1,2	83.6	126.4	<0.001	1	75.1	344.2	<0.001	1,2	81.9	220.9	<0.001
Altitude	1,2	16.8	6.0	0.005	2	13.1	18.1	<0.001	2	37.7	59.6	<0.001

Dependent Variable	Lower Alpine (n=116)				Upper Alpine (n=19)			
	Terms Required	r^2	F	p	Terms Required	r^2	F	p
Drainage score	1	75.0	346.0	<0.001	1	54.7	22.8	<0.001
Altitude	1,2	39.0	37.7	<0.001	No reasonable model			

Table 9.2 The results of multiple regressions of site characteristics on combinations of DCA ordination axes, for the five altitudinal sub-sets. Each ordination was performed on cover class data for 100 m^2 samples. For explanations of r^2, F and p, see the caption of Table 9.1.

on the drainage gradient within each altitudinal belt. In the middle subalpine and the two alpine zones, quadrat scores on axis 1 would be sufficient for this purpose (cf. Peet 1981). In the other two zones, more satisfactory indices could be obtained by projection of quadrats onto a line slightly oblique to the first axis. Miller, Shepard and Chang (1964) have presented a method by which the most appropriate direction for such a line could be determined.

Having determined indirect drainage scores for quadrats within each altitudinal belt, it would then be necessary to adjust the scaling of the scores within each altitudinal sub-set to make them comparable between sub-sets. Peet (1981) has described a possible approach to this problem. Finally, the rescaled indirect drainage scores could be used, in combination with altitude, to construct a two-dimensional gradient analysis. This approach was not explored in the present study. A primary objective of the direct gradient analysis (Chapter 8) was to obtain observational evidence concerning the nature of vegetational response to environmental gradients. Such evidence was required for the formulation of the vegetation-gradient models used in Part 1 of this thesis. If an drainage index, based on DCA, had been employed, an undesirable element of logical circularity would have been introduced.

Plots showing the distribution of altitude on the two-dimensional quadrat ordination for each altitudinal sub-set (not given), suggested a relationship between the second ordination axis and altitude for all except the upper alpine sub-set. The relationships were described by linear regressions of altitude on axis 2 for the middle and upper subalpine and the lower alpine sub-sets. Both axis 1 and axis 2 were required for the lower subalpine sub-set (Table 9.2). Although the

regressions were all statistically significant, the adjusted r^2 values were relatively low (less than 40%). Since the quadrats in each sub-set span an altitudinal range of only 100m, the poor recovery of the altitudinal gradient in these ordinations may be attributable to the increased vulnerability of DCA to noise variation at low beta diversities.

For the lower and upper subalpine sub-sets, another factor contributing to the relatively weak relationship between the second ordination axis and altitude was identified. In the ordination of the upper subalpine sub-set, variation along the second axis is largely confined to quadrats located towards the lower (i.e. waterlogged) end of the first axis (Figure 9.10c). Samples at the upper (i.e. well drained) end of the first axis display little variation along the second axis, even though they span the full range of altitude covered by this sub-set. These quadrats are separated on the third ordination axis. Examination of a stereogram (not given) revealed that the rectangular coenoplane related to drainage and altitude had been twisted through 90° near the middle of its longer axis in the DCA ordination. The ordination thus used three axes to describe a compositional pattern which is intrinsically two-dimensional. A similar phenomenon was apparent in the ordination of the lower subalpine sub-set (Figure 9.10a).

Distortion of this kind occurred in the DCA ordinations of some of the rectangular coenoplane models examined in Chapter 4, even in the absence of noise (e.g. Figure 4.1, centre left panel). The ability of DCA to twist rectangular compositional patterns in this manner has not

been previously reported. The mechanism which gives rise to such distortion is not understood at present. Users of DCA should be aware of the possibility that such distortion of rectangular coenoplanes may occur.

In the ordination of the upper alpine sub-set (Figure 9.11b), the second axis was not related to altitude. This is hardly surprising, since the quadrats in this sub-set covered an altitude range of only 60m and all but four of them had altitudes in the top quarter of this range (1355-1370m). A consideration of the topographic positions of the quadrats suggested that the compositional gradient represented by the second axis may be related to the duration of snow-lie. The five quadrats with highest scores on axis 2 are all located just below the top of east to north-east facing slopes. Since the prevailing winds are west to south-westerlies, snow cornices tend to form in such situations and small snow patches often persist until late spring. Samples with scores towards the other end of axis 2 are generally in more exposed situations, where snow-lie is of shorter duration. Species whose occurrences are concentrated towards the upper end of the second axis include the prostrate shrub Gaultheria depressa, the herbs Cheesemannia radicata and Epilobium gunnianum and the fern Blechnum penna-marina. The compositional gradient related to snow-lie was not apparent in the DCA ordination of the total data set. It may have been revealed if it had been possible to extract more than four axes.

The DCA ordinations of the five altitudinal sub-sets have confirmed that the major direction of compositional variation within each altitudinal belt is related to the drainage gradient. Furthermore, the analyses showed that compositional variation along the drainage

gradient is relatively continuous. They did not support the notion that the use of the crude, five class drainage scale in the direct gradient analysis blurred or masked compositional discontinuities. The ordinations of the altitudinal sub-sets also illustrated some of the undesirable properties of DCA as an indirect gradient analysis technique, which had previously been recognised in the simulation study. The mechanisms responsible for these distortions require further investigation.

9.3.6 Beta Diversity and the Scaling of DCA Ordinations

The scaling of axes in DCA is such that the range of quadrat scores along a given axis should provide an estimate of the beta diversity of the compositional gradient represented by that axis (Hill and Gauch 1980). The units of axis scaling in DCA (as implemented in the program DECORANA) should theoretically approximate the Z units of Gauch and Whittaker (1972a), where 1Z is the length of a coenocline segment corresponding to the average standard deviation of the (Gaussian) species abundance profiles. Hill and Gauch (1980) recommended the use of the term "sd" (standard deviation) in preference to Z, since it is more explicit. They found that the lengths of the first axes in DCA ordinations of simulated Gaussian coenoclines generally underestimated the beta diversity of the artificial gradients by 10-20%. Similar results were obtained in the present simulation study.

Direct estimates of the beta diversity of the drainage gradient within each of five altitudinal belts on the Mt. Field Plateau have been presented in Table 8.7. These were expressed in half-changes (HC) of

the percentage similarity coefficient and the Sorenson coefficient. Both sets of values indicated a systematic decline in the beta diversity along the drainage gradient with increasing altitude. However, neither of these sets of beta diversity values is strictly comparable with the indirect estimates provided by the DCA ordinations of the altitudinal sub-sets, since the ordinations were based on integer cover class data. For the purpose of the comparison, a further set of beta diversities was computed, in the manner described in section 8.2.2, using percentage similarities calculated from cover class data. The resulting values (Table 9.3) were intermediate in magnitude to those based on midpoint percentage cover data and those computed from presence-absence data (Table 8.7).

For each altitudinal belt, the range of quadrat scores on the first axis of the DCA ordination was taken as an indirect estimate of the beta diversity of the drainage gradient, expressed in sd units (Table 9.3). In the case of the lower and upper subalpine sub-sets, where the recovered drainage gradient was slightly oblique to axis 1, beta diversity would be more correctly estimated by projecting the quadrats onto an oblique axis. However, in view of the relatively small angle involved, the error introduced by simply using the scores on axis 1 was considered negligible.

The direct estimates of beta diversity display a monotonic decrease with increasing altitude. The low value for the upper alpine belt is partly due to the absence of any quadrats in drainage classes 1 and 2. The indirect estimates also tend to decline with increasing altitude, although the value for the upper subalpine belt is slightly

Limits of Altitude Belt (m)	Estimates of the Beta Diversity of the Drainage Gradient		
	Direct Estimate in HC of the Percentage Similarity Coefficient (cover class data)	Length of First Axis in DCA Ordination of Altitudinal Sub-set ("sd" units)	Distance Between Centroids of Water-logged and Boulderfield Quadrats in DCA Ordination ("sd" units)
910 - 1010	3.5	4.5	3.7
1011 - 1110	2.7	3.8	2.9
1111 - 1210	2.6	4.0	2.7
1211 - 1310	2.1	3.5	2.2
>1310	1.5	2.4	1.4

Table 9.3 A comparison of indirect estimates of the beta diversity of the drainage gradient within five altitudinal belts, with direct estimates. The direct estimates are expressed in half-changes (HC) of the percentage similarity coefficient, computed between the centroids of samples in each drainage class. The indirect estimates are based on inter-sample distances measured in the DCA ordinations of the five altitudinal sub-sets (cover class data). The scaling of axes in DCA is such that ordination distances should provide estimates of beta diversity in "sd" units.

greater than the figure for the middle subalpine. The indirect estimates are 30 to 70% greater than the corresponding direct estimates.

The relationship between sd or Z units and half-changes (HC) of the percentage similarity coefficient has been investigated by Gauch (see Gauch and Whittaker 1972a), using simulated coenoclines. For noiseless data derived from a simple Gaussian coenocline, in which the species optima are equally spaced and modal heights are equal, 1HC is equal to 1.349sd. Hill and Gauch (1980) suggest that, for real data, the ratio between sd and HC units is usually smaller, and may approach unity. If so, the discrepancy between sd and HC units is insufficient to account for the observed differences between indirect beta diversity estimates (sd) and the direct estimates (HC) for the altitudinal sub-sets.

The direct beta diversity values are almost certainly underestimates. Their computation is based on the average composition of groups of quadrats within each of the five drainage classes. The composite quadrats for drainage classes 1 and 5 express the average composition of the quadrats within extreme segments of the drainage gradient, rather than the composition of quadrats located at the extremes of the gradient. In contrast, the lengths of the DCA axes are based on data for individual quadrats, which potentially span the full range of the drainage gradient. This may be the major reason for the discrepancy between the direct and indirect estimates. The distance between the centroid of the quadrats in drainage class 1 and the centroid of those in drainage class 5 was measured in the space defined by the first two axes of each DCA ordination. The resulting values, which are expressed in sd units, are given in Table 9.3. These values

were very similar to the direct estimates of beta diversity.

It thus appears that the length of DCA quadrat ordinations can provide a useful measure of beta diversity. Experiments with simulated coenoclines have shown that (a) DCA tends to underestimate the sd length of gradients by 10-20% and (b) beta diversity values in sd units may be up to 35% greater than values based on half-changes of percentage similarity. The present results suggest that, in the analysis of field data, the opposing effects of these two phenomena may result in the sd values from DCA ordinations being similar in magnitude to half-changes of percentage similarity.

9.3.7 Comparison of Ordination Methods

The ordinations of the total compound data set (60 cluster centroids) by DCA, using cover class and presence-absence data, were very similar to the corresponding DCA ordinations of the individual quadrat data, and to each other. The distributions of mean drainage score and mean altitude on the first two axes of the cover class ordination of the total compound data set are shown in Figure 9.12. These plots may be compared with Figures 9.2 and 9.3. The third axis of both the cover class and presence-absence ordinations of the compound-quadrats was a spurious "interaction" axis. The fourth axis in each case represented the compositional gradient among subalpine forests on well drained sites, which has been tentatively related to firing history (section 9.3.1). The reduction of the full set of 398 quadrats to 60 clusters thus appears to have retained sufficient compositional variation to permit the recovery of the major underlying gradients. The results of multiple regressions of mean altitude and mean drainage score

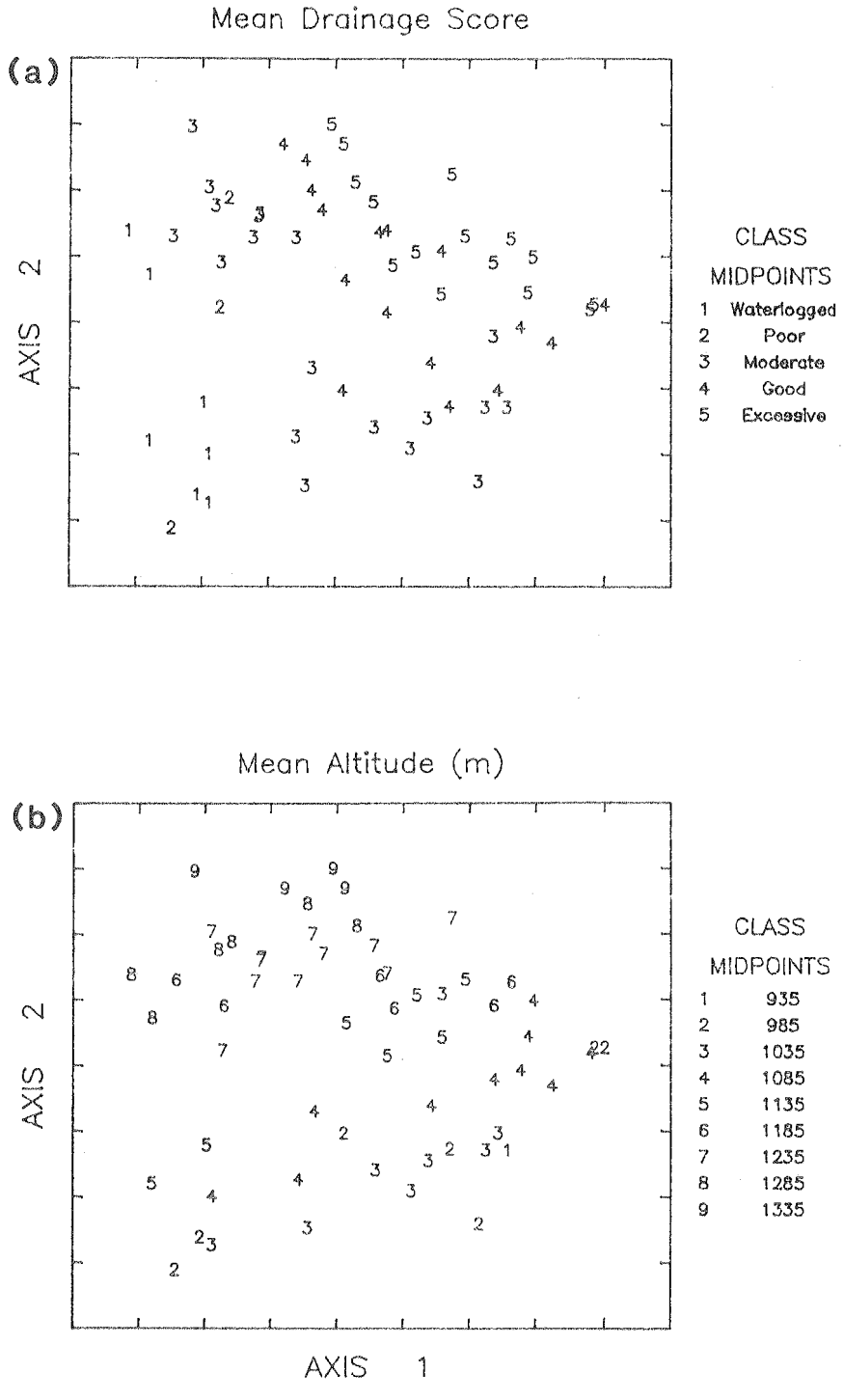


Figure 9.12 The distributions of (a) mean drainage score (rounded to five classes) and (b) mean altitude (rounded to nine classes) within the compound-quadrat configuration defined by axes 1 and 2 of the quantitative DCA ordination of the total compound data set (mean cover class data). The 60 compound-quadrats are the centroids of the 60 group classification of the total data set produced by Minimum Sum-of-Squares Clustering of a matrix of chord distances.

Dependent Variable	DCA: mean cover class data				DCA: presence-absence data				LNMDS: 3-D, percentage similarity			
	Terms Required	r^2	F	p	Terms Required	r^2	F	p	Terms Required	r^2	F	p
Drainage score	$1,1^2,2,2^2,1x2$	87.1	80.7	<0.001	$1,1^2,2,2^2$	84.0	78.5	<0.001	$1,1^2,2$	86.3	124.9	<0.001
Altitude	$1,1^2,2$	89.5	168.3	<0.001	1,2	90.9	295.3	<0.001	1,2	88.1	218.5	<0.001

Dependent Variable	GNMDS: 3-D, percentage similarity				LNMDS: 2-D, percentage similarity				LNMDS: 2-D, Sorenson coefficient			
	Terms Required	r^2	F	p	Terms Required	r^2	F	p	Terms Required	r^2	F	p
Drainage score	$1,1^2,2$	86.3	125.0	<0.001	$1,1^2,2$	85.5	117.3	<0.001	$1,1^2,2$	82.0	90.5	<0.001
Altitude	1,2	88.1	218.5	<0.001	1,2	87.4	204.7	<0.001	1,2	89.3	248.1	<0.001

Dependent Variable	PCoA: percentage similarity				PCA-C: mean cover class data				PCA-CS: mean cover class data			
	Terms Required	r^2	F	p	Terms Required	r^2	F	p	Terms Required	r^2	F	p
Drainage score	$1,1^2,2$	84.3	106.4	<0.001	$1,1^2,2$	84.1	105.1	<0.001	$1,1^2,2,1x2$	83.5	75.4	<0.001
Altitude	1,2	79.6	116.1	<0.001	1,2,1x2	74.2	57.6	<0.001	1,2	77.2	100.7	<0.001

Table 9.4 The results of multiple regressions of mean site characteristics on combinations of ordination axes, for various ordinations of the total compound data set (centroids of 60 minimum sum-of-squares clusters). For explanations of r^2, F and p, see the caption of Table 9.1.

on polynomial functions of the first two axes of both the cover class and presence-absence ordinations are given in Table 9.4. The adjusted r^2 values are considerably greater than those obtained for the corresponding DCA ordinations of the total data set (Table 9.1). This improvement in predictivity may be attributed to the smoothing of noise variation associated with the averaging of both species and environmental data.

LNMDS in three dimensions, using compound-quadrat scores on axes 1,2 and 4 of the DCA cover class ordination as a starting configuration and operating on a matrix of percentage similarity coefficients, reached a minimum stress of 4.9% in 27 iterations. The distributions of mean drainage score and mean altitude on the first two axes of the resulting ordination are shown in Figure 9.13. The patterns are broadly similar to those observed in the DCA cover class ordination (Figure 9.12). The ordinations differ primarily in matters of local detail. For example, LNMDS emphasises the distinctiveness of two two high altitude, excessively drained compound-quadrats at the upper right of the ordination. The distance between alpine and subalpine compound-quadrats at the waterlogged extreme of the drainage gradient is somewhat less in the LNMDS ordination than in the DCA ordination. Procrustean analysis showed that the RMS displacement between corresponding points in the LNMDS and DCA ordinations was equal to about 8% of the range of compound-quadrat scores on the first DCA axis. Regressions of mean drainage score and mean altitude on the first two axes of the LNMDS ordination (Table 9.4) had adjusted r^2 values very close to those obtained for the DCA cover class ordination. On this basis, therefore, no difference in the performance of LNMDS relative to DCA could be

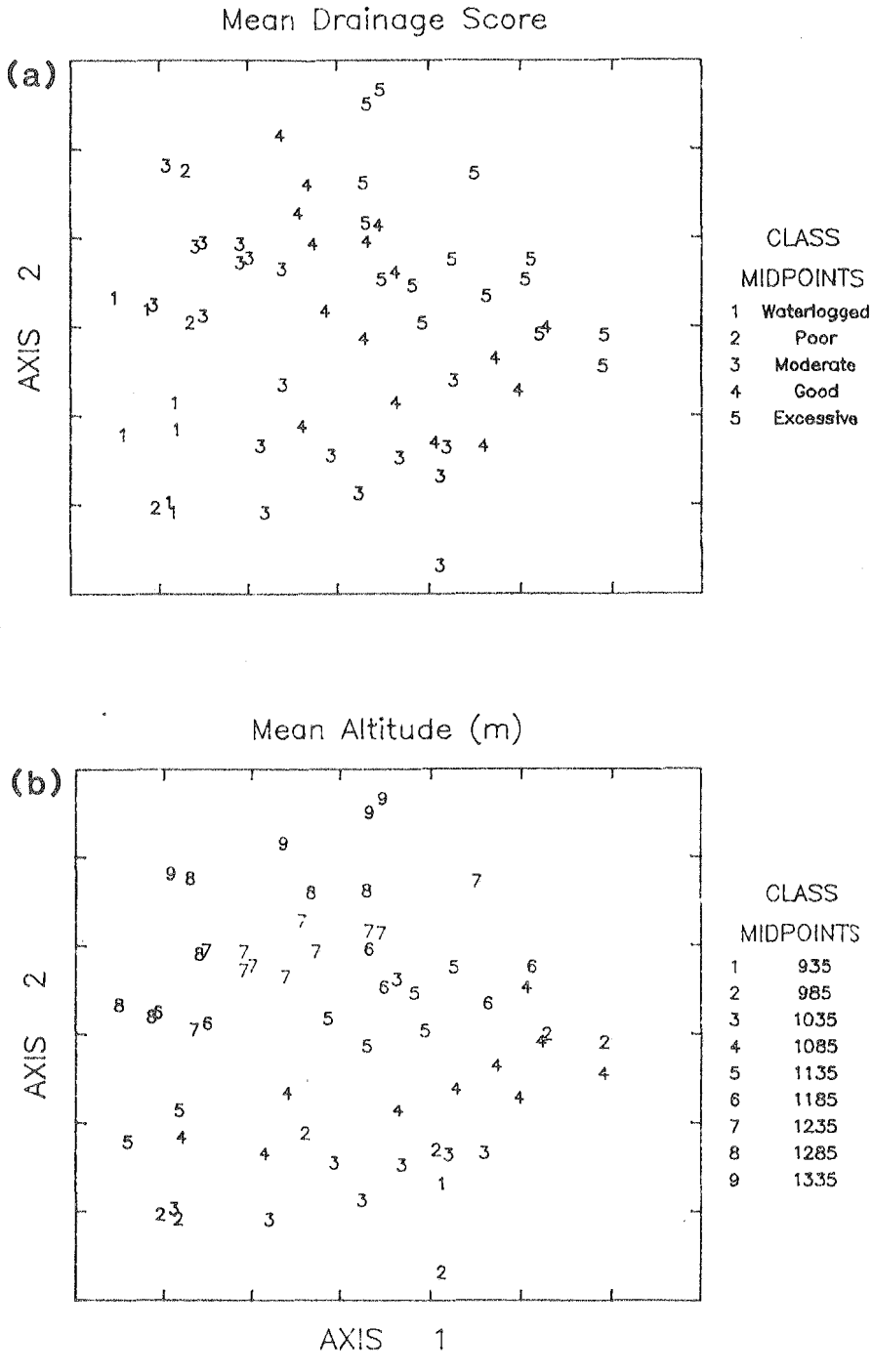


Figure 9.13 The distributions of (a) mean drainage score (rounded to five classes) and (b) mean altitude (rounded to nine classes) within the compound-quadrat configuration defined by axes 1 and 2 of the three-dimensional Local Non-metric Multidimensional Scaling (LNMDS) ordination of the total compound data set. LNMDS was based on a matrix of percentage similarity coefficients, computed between each pair of compound-quadrats. Compound-quadrat scores on axes 1,2 and 4 of the quantitative DCA ordination were used as an initial configuration.

detected. The third axis of the LNMDS ordination arranged the compound-quadrats in a similar manner to the fourth axis of the DCA ordination, once again differing only in detail.

LNMDS in two dimensions, using a percentage similarity matrix and starting with compound-quadrat scores on axes 1 and 2 of the DCA ordination, achieved a minimum stress of 7.6% in 16 iterations. The resulting ordination was very similar to the configuration on the first two axes of the three-dimensional LNMDS solution. Regressions of mean drainage score and mean altitude on the ordination axes produced adjusted r^2 values only marginally lower than those obtained for both the three-dimensional LNMDS and DCA ordinations (Table 9.4).

A two-dimensional LNMDS, based on a matrix of Sorenson coefficients and using a DCA starting configuration, attained a minimum stress of 8.3% in 17 iterations. The arrangement of compound quadrats in this ordination was similar to that on the first two axes of the LNMDS ordinations based on percentage similarity. A regression of mean drainage score on the ordination axes yielded an adjusted r^2 somewhat lower than the value obtained for the previous LNMDS ordinations (Table 9.4). However, the adjusted r^2 for a regression of mean altitude on the ordination axes was slightly greater than the value obtained for the LNMDS ordinations based on percentage similarity. This analysis once again shows that sufficient information to enable effective recovery of underlying gradients can be obtained from presence-absence data, provided that the beta diversity of the gradients is sufficiently high.

Global Non-metric Multidimensional Scaling (GNMDS) in three-dimensions reached a minimum stress of 7.2% in 25 iterations. The

resulting ordination was extremely similar to the three-dimensional LNMDS solution. Procrustean analysis showed that the RMS displacement between corresponding points in the two ordinations was of the order of only 2% of the range of scores on the first axis. The high degree of concordance between the GNMDS and LNMDS ordinations is also reflected in the results of multiple regressions of mean drainage score and altitude on the first two axes of the GNMDS ordination (Table 9.4). The fitted equations and r^2 values were virtually identical to those obtained for the LNMDS ordination. Thus "local" and "global" rank order criteria define very similar solutions for this data set. The theoretical attraction of the "local" criterion is that it allows for the possibility that the form of the monotonic relationship between compositional similarity and ecological separation (i.e. ordination distance) may vary from point to point within a compositional pattern (cf. Prentice 1980). The similarity between global and local solutions in the present case suggests that such point to point variation is not a feature of the vegetational continuum on the Mt. Field Plateau.

The PCoA ordination of the total compound data set, operating on a matrix of percentage similarity coefficients, represented the coenoplane related to altitude and drainage as a dome-shaped surface on its first three axes. The edges and corners of the coenoplane were folded inwards towards the centre of the ordination. Consequently, the first two axes, which accounted for 32.4% of the total variation, provided only a crude representation of the two major underlying gradients. The distribution of mean altitude with respect to axes 1 v. 2 and 1 v. 3 is shown in Figure 9.14, and a stereogram illustrating compound-quadrat locations on the first three axes is presented as Figure 9.15a. These diagrams

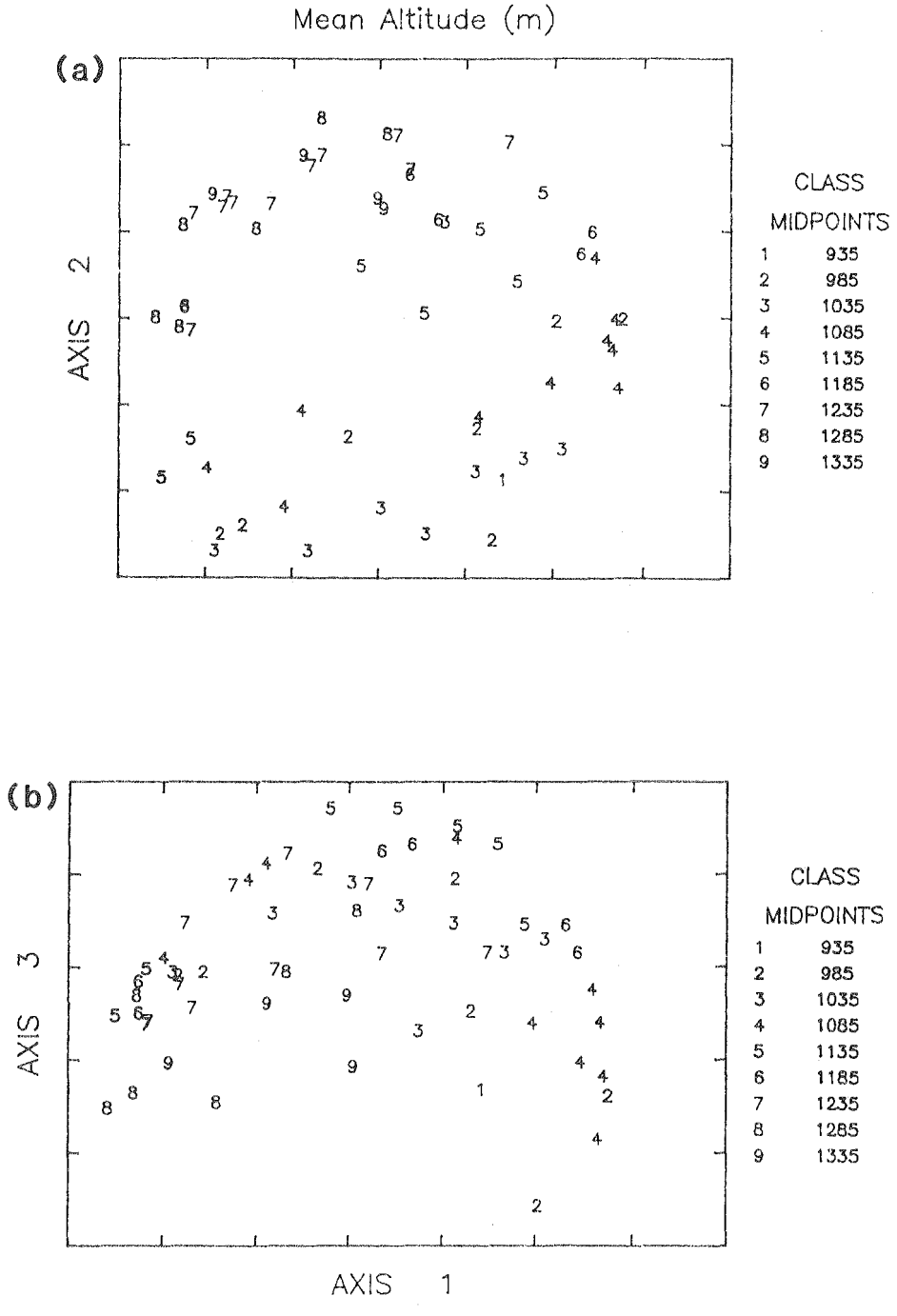


Figure 9.14 The distribution of mean altitude (rounded to nine classes) within the compound-quadrat configurations defined by (a) axes 1 and 2 and (b) axes 1 and 3 of the PCoA ordination of the total compound data set. Involution of compound-quadrats at the extremes of the altitudinal gradient, due to severe curvilinear distortion of the altitude versus drainge coenoplane, is apparent.

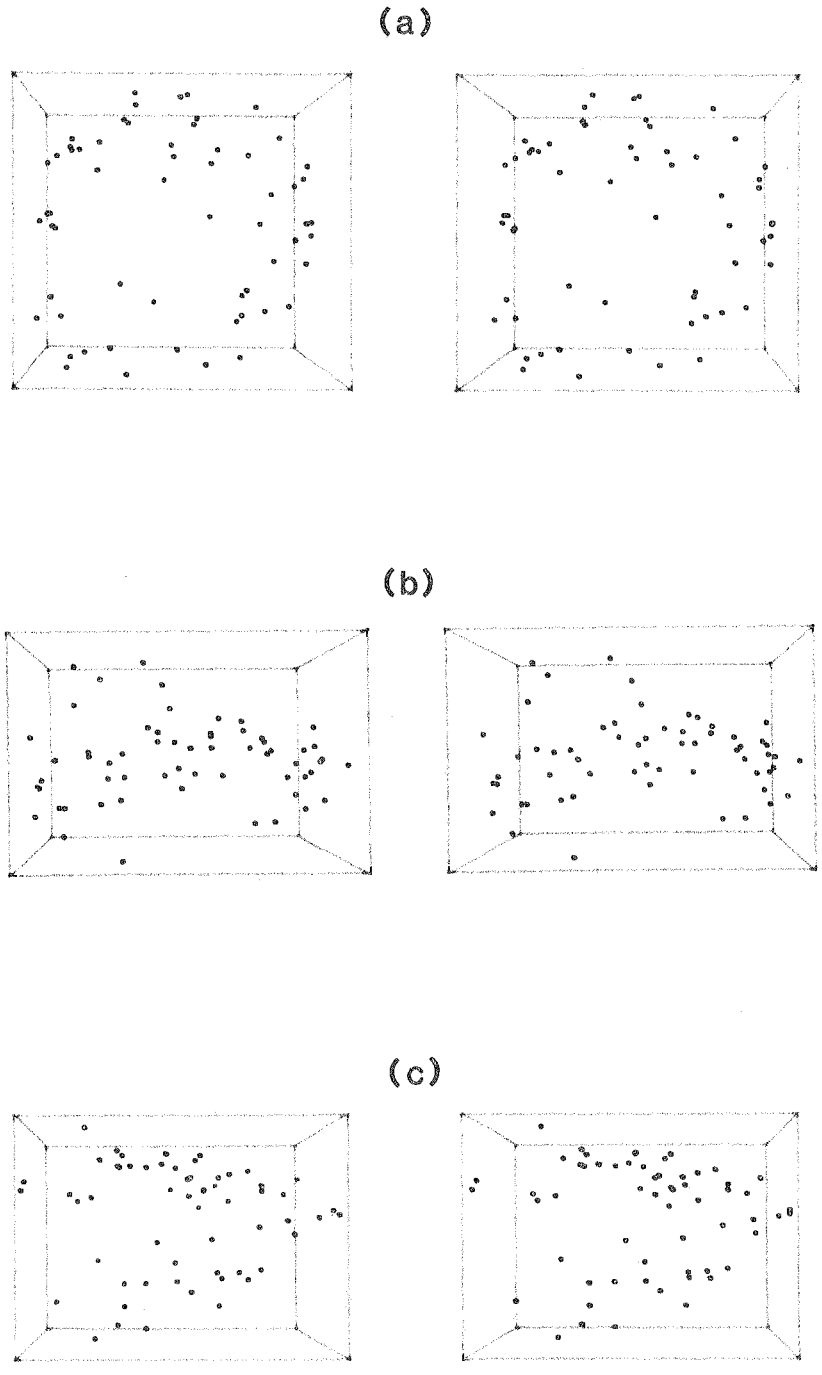


Figure 9.15 Stereograms showing the positions of compound-quadrats with respect to selected sets of three axes in ordinations of the total compound data set. Diagrams (a) and (b) refer to the PCoA ordination, while (c) illustrates some results of the PCA-CS ordination. The identities of the X (horizontal), Y (vertical) and Z (normal to the paper) axes are as follows: (a) X=1, Y=2, Z=3; (b) X=1, Y=6, Z=2; (c) X=1, Y=2, Z=3.

clearly illustrate the involution of the compound-quadrats in the highest and lowest altitude classes.

Axes 4 and 5 of the PCoA ordination merely represented further components of the curvilinear distortion of the altitude X drainage coenoplane. It was not until the sixth axis that the ordination recovered the compositional variation related to the supposed "firing history" gradient. The sixth axis separated the compound-quadrats representing opposite extremes of this gradient from the remainder, but also described further curvilinear distortion of the altitude X drainage coenoplane.

Of the three PCA variants examined, PCA-C and PCA-BC produced ordinations similar to the PCoA solution. Both were marred by curvilinear distortion and involution of the altitude X drainage coenoplane. Recognition of the "firing history" gradient was delayed until the sixth or seventh axis. In the PCA-C ordination, the sixth axis separated compound-quadrats at the rainforest/mixed forest end of the firing history gradient from the remainder, but the separation of the compound-quadrat at the opposite extreme of the "firing history" gradient was masked by residual curvilinear distortion of the altitude X drainage coenoplane. The distinctiveness of this compound-quadrat did not become apparent until it was separated on the seventh axis. PCA-C therefore required two axes to effectively represent the "firing history" gradient. This shows that curvilinear distortion of major compositional gradients by methods such as PCA-C can interfere with the effective recovery of further, relatively minor, gradients.

PCA-CS was less affected by curvilinear distortion than the other

two PCA variants and PCoA. Nevertheless, the distortion was sufficiently severe to result in slight involution of the extremes of both the altitude and drainage gradients on the first two axes. A stereogram showing compound-quadrat locations on the first three axes is presented as Figure 9.15c. The "firing history" gradient was approximately recovered on axis 5, together with some residual curvilinear distortion of the altitude X drainage coenoplane.

Multiple regressions of mean drainage score and mean altitude on polynomial functions of the first two axes of the PCoA and PCA ordinations (Table 9.4), had adjusted r^2 values considerably lower than those obtained for the DCA and NMDS ordinations. The lower predictivity of the PCoA and PCA ordinations is the result of the curvilinear distortion and involution of the altitude X drainage coenoplane. The altitude regressions were most seriously affected, with r^2 values of 74-80%, compared with the figures of 88-91% obtained for the DCA and NMDS ordinations.

The results of the PCoA and PCA ordinations show that the curvilinear distortion of major compositional gradients (the "type A" distortion of Orloci 1974a) can interfere with the effective recovery of further, relatively minor gradients. In each case, recovery of the "firing history" gradient was delayed until the fifth or sixth axis by residual components of the curvilinear distortion. PCoA was more successful than the PCA variants in recovering the "firing history" gradient. Figure 9.15b shows the compound-quadrat configuration on axes 1,6 and 2 of the PCoA ordination. Although axis 6 effectively separates the extremes of the "firing history" gradient, a considerable amount of

variation on axis 6 is still due to curvilinear distortion of the major coenoplane. This type of interference with the effective recovery of minor compositional gradients is one of the most serious consequences of type A distortion. Often the identity of the major compositional gradients and their underlying environmental relationships is known, or at least suspected, before an ordination is performed. Ordination should help to clarify the nature of such gradients and correct any prior misconceptions. In addition, an effective ordination is expected to reveal other compositional gradients which may not have been obvious before the analysis. If curvilinear distortion of the "known" gradients hampers recognition of such "unsuspected" gradients, the value of ordination as a heuristic tool is severely impaired.

Critics of Non-metric Multidimensional Scaling techniques (e.g. J.C.Gower in Sibson 1972) often point out that NMDS can only function because the ranked similarities contain a large amount of metric information. Consequently, they claim that metric and non-metric scaling solutions are usually similar, although the latter require far more computation. Gauch, Whittaker and Singer (1981) seem to support this view. The present analyses illustrate the danger of such generalisations. The LNMDS and GNMDS ordinations may be directly compared with the metric ordination produced by PCoA, since they all operated on a matrix of percentage similarity coefficients. The non-metric and metric solutions differ substantially, and the former must be regarded as markedly superior for the purpose of indirect gradient analysis. Non-metric and metric criteria will only lead to similar solutions when the relationship between sample similarity and sample separation along underlying gradients is approximately linear.

In the context of indirect gradient analysis, this will only be true when the beta diversity of such gradients is low. The notion that the results of non-metric and metric ordinations are generally similar has arisen from experience with data sets in which the relationships between variables and the underlying gradients of interest were linear, or at least monotonic.

In summary, the comparative application of ordination methods to the total compound data set has confirmed the superiority of DCA and NMDS over PCoA and PCA, for the purpose of indirect gradient analysis.

9.3.8 Analysis of Recently Burnt Alpine Sites

The disposition of the 15 alpine burnt quadrats on the first two axes of the DCA ordination is shown in Figure 9.16a. Axis 1 (eigenvalue=0.307) separates the six quadrats on the Tarn Shelf, which were burnt in 1966, from the Mawson Plateau quadrats burnt in 1961. The compositional differences between these two groups of quadrats are unlikely to result from the five year difference in time since burning, since compositional variation between Mawson Plateau and Tarn Shelf is also apparent among unburnt quadrats (see below). One major environmental factor which distinguishes the two areas is the degree of exposure to the prevailing west to south-westerly winds. The Mawson Plateau sites, located along the south-west margin of the plateau, are highly exposed, while the Tarn Shelf sites are protected from the full force of south-westerly gales by the Rodway Range. Apart from direct effects, such as damage to foliage and increased evapotranspiration rates, the degree of wind exposure also influences patterns of snow accumulation.

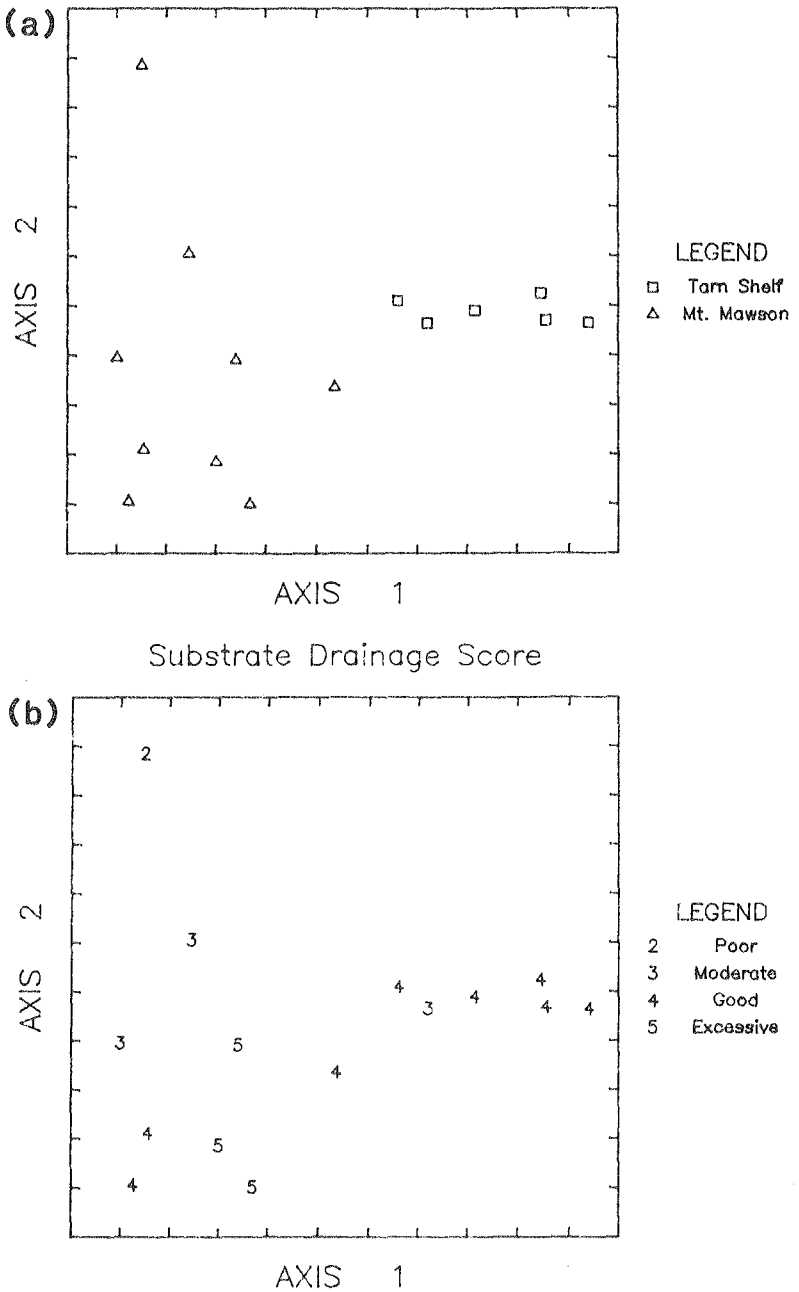


Figure 9.16 The quadrat configuration defined by axes 1 and 2 of the DCA ordination of the 15 burnt alpine samples. In (a) the triangles (△) indicate quadrats located on Mawson Plateau, which were burnt in 1961, while the squares (□) indicate quadrats from Tarn Shelf, burnt in 1966. The distribution of drainage scores on the ordination is shown in (b).

The second axis (eigenvalue=0.146) represents a compositional gradient among the Mawson Plateau quadrats which is closely related to drainage (Figure 9.16b). The Tarn Shelf quadrats were relatively uniform in drainage conditions. Further axes had relatively small eigenvalues and were not interpretable.

The DCA ordination of the paired burnt and unburnt quadrats yielded three interpretable axes with eigenvalues of 0.329, 0.176 and 0.098. The configuration of quadrats on the first three axes is shown in Figure 9.17, where each unburnt quadrat is connected to its paired burnt quadrat by an arrow. In combination, axes 1 and 2 separate the Mawson Plateau quadrats, both burnt and unburnt, from the Tarn Shelf quadrats. This suggests that the compositional divergence between the post-fire vegetation of the two regions (Figure 9.16a) is not simply attributable to the five year difference in time since burning. The distribution of drainage scores on the first two axes of the ordination is shown in Figure 9.18. There is a marked tendency for drainage scores to increase across ordination, from upper right to lower left. The Tarn Shelf quadrats, which span a only a short segment of the drainage gradient, have been correctly placed within this diagonal trend.

In the compositional space defined by the first two axes, the arrows joining unburnt quadrats to their corresponding burnt quadrats tend to converge, so that both groups of burnt quadrats are less scattered along the diagonal "drainage" gradient than the unburnt quadrats (Figure 9.17a). This agrees with the assertion of Kirkpatrick, Dickinson and Cantle (1982), that fire in Tasmanian alpine communities tends to decrease the degree of compositional heterogeneity among sites.

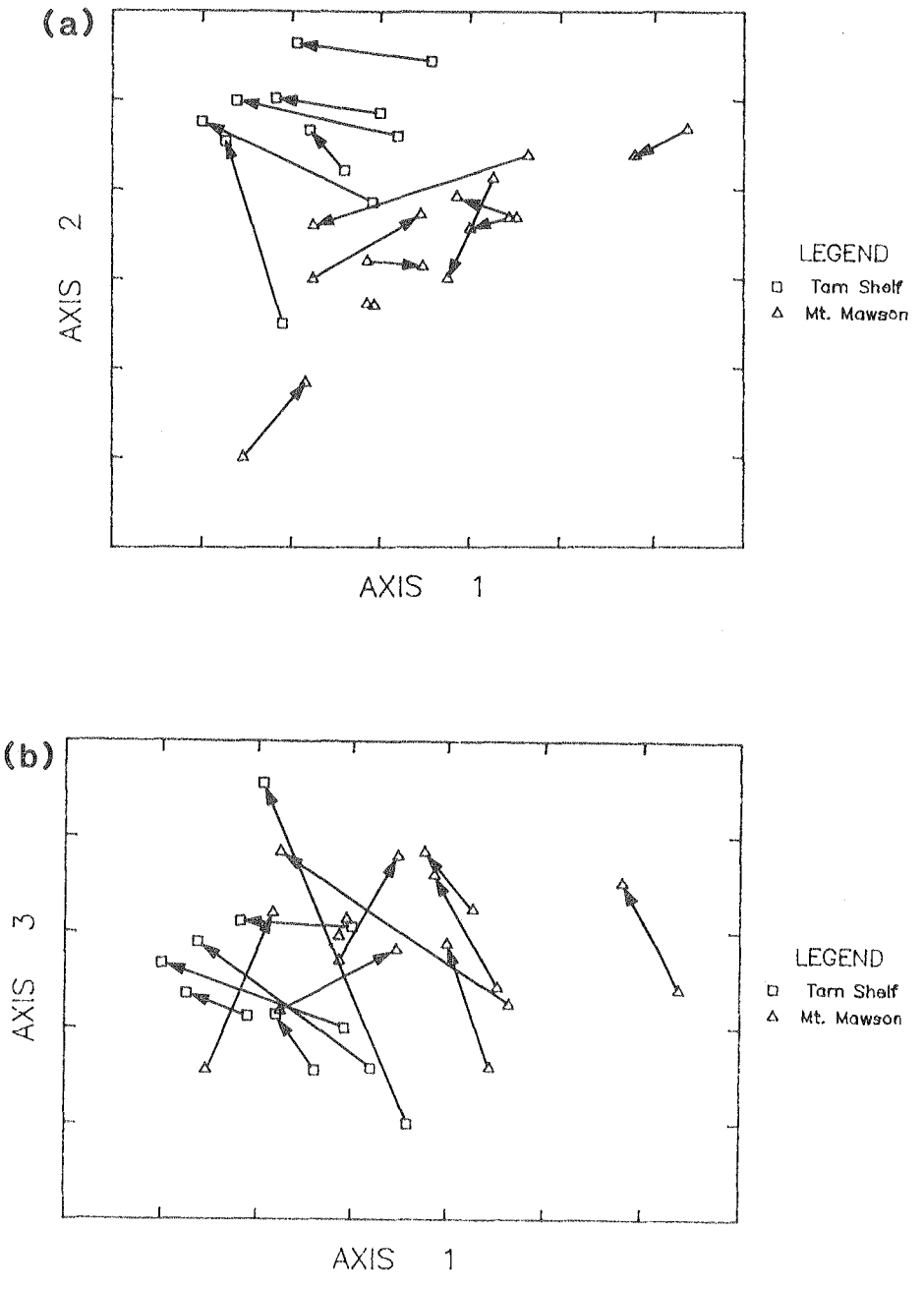


Figure 9.17 The configurations of quadrats with respect to (a) axes 1 and 2 and (b) axes 1 and 3 of the DCA ordination of paired burnt and unburnt alpine samples. Each unburnt quadrat is joined to its burnt companion by an arrow. Triangles(△) indicate Mawson Plateau quadrats, while Tarn Shelf quadrats are represented as squares (□).

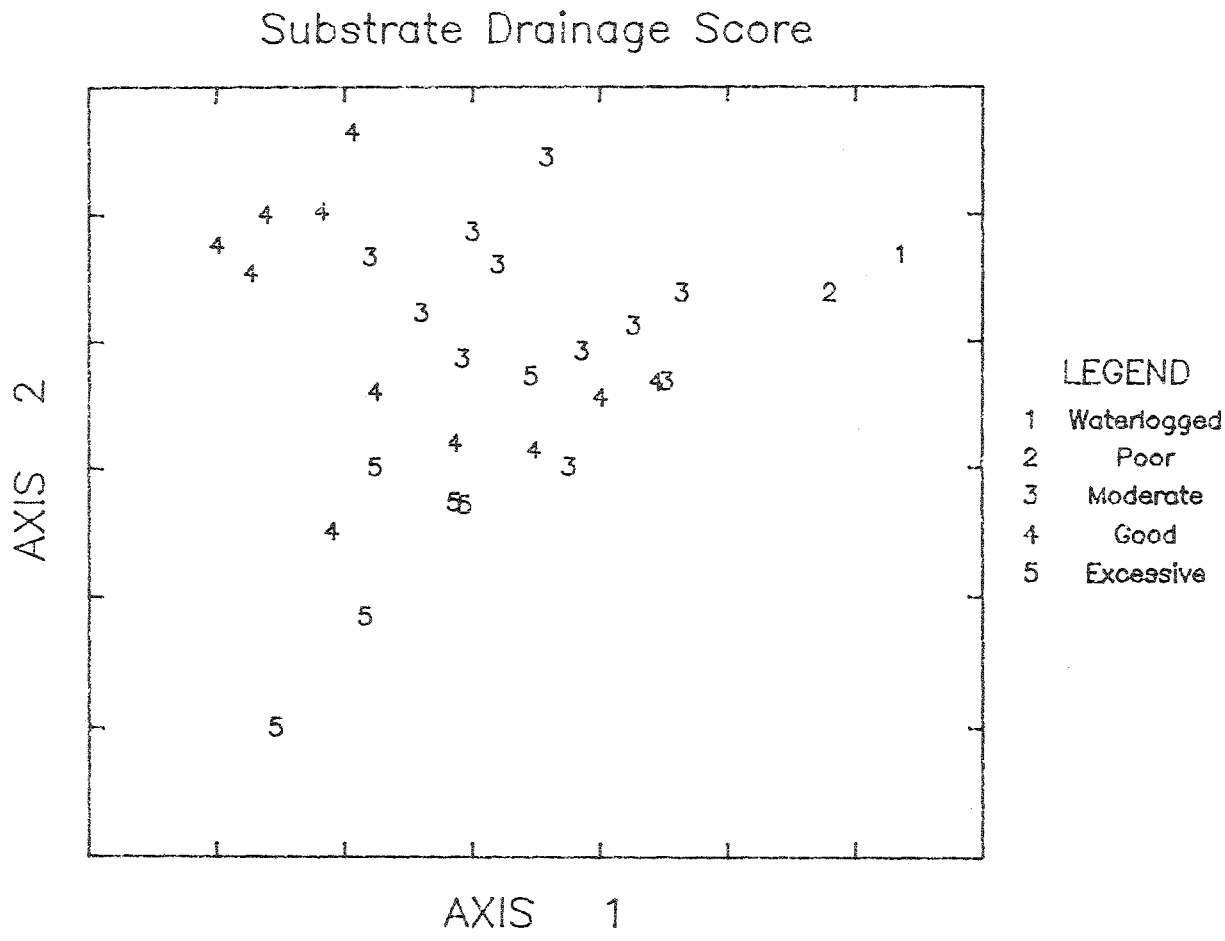


Figure 9.18 The distribution of drainage score within the configuration of quadrats defined by axes 1 and 2 of the DCA ordination of the paired burnt and unburnt alpine quadrats. Note the gradation of drainage scores from upper right to lower left.

In the present case, the compositional convergence primarily reflects a reduction in beta diversity along the drainage gradient among the burnt sites. The species which predominate on the burnt sites, such as Astelia alpina, Poa gunnii and Helichrysum backhousii, are most abundant under intermediate drainage conditions in the unburnt vegetation (see Appendix C).

There is no apparent tendency for post-fire convergence in vegetational composition between the two regions. In fact, the ordination suggests that the pre-fire vegetation on Tarn Shelf has closer affinities with Mawson Plateau than the post-fire vegetation (Figure 9.17a). The burnt Tarn Shelf quadrats are concentrated at the upper left of the ordination. The compositional divergence between the burnt Tarn Shelf quadrats and the burnt Mawson Plateau quadrats with similar drainage scores (i.e. 3 to 4) may be attributed to (a) the deterministic effects of other environmental factors (e.g. wind exposure) and (b) stochastic variability in the dispersal and establishment of "fire-weed" species (e.g. Senecio gunnii).

The third axis of the ordination separates the burnt quadrats in both regions from their paired unburnt quadrats. Almost without exception, the burnt quadrats have higher scores on axis 3 than their corresponding unburnt quadrats (Figure 9.17b). The third axis thus describes the general direction of compositional change after burning. In fact, the arrows joining unburnt and burnt quadrats are generally oblique to axis 3, so that the fire-related compositional gradient extends diagonally across Figure 9.17b. An inspection of the species ordination (not shown) revealed that species regarded as fire sensitive are concentrated towards the lower right of the ordination on axes 1 and

3. These include the conifers Athrotaxis cupressoides, Diselma archeri, Microstrobos niphophilus, Microcachrys tetragona and Podocarpus lawrencii and the shrubs Orites acicularis, Trochocarpa cunninghamii and Archeria comberi (Kirkpatrick 1980; Kirkpatrick, Dickinson and Cantle 1982). The upper right of the ordination (i.e. the "burnt" extreme of the compositional gradient) is characterised by herbs and graminoids, including Scaevola hookeri, Senecio gunnii, Danthonia fortuna-hibernae, Ewartia planchonii and Epilobium sarmentaceum and by shrubs with either efficient seed dispersal (e.g. the composite Helichrysum backhousii) or the ability to recover vegetatively after fire (e.g. Orites revoluta, Richea sprengelioides).

This analysis is regarded as preliminary. The number of quadrats is small and the basis upon which unburnt quadrats were selected for pairing with the burnt quadrats may be questioned. The assumption that the vegetation of each unburnt quadrat is representative of the pre-fire vegetation on its paired burnt quadrat may not be fully justified. The quadrats were not originally collected with the present analysis in mind. A more appropriate sampling strategy for this type of study would be to take quadrats on opposite sides of recognisable fire boundaries (cf. Kirkpatrick, Dickinson and Cantle 1982). However, despite these practical limitations, the analysis serves to demonstrate the potential value of ordination in the study of vegetational response to disturbance (cf. Austin 1977). The three-dimensional DCA ordination provided a useful summary of the major trends of compositional variation among the quadrats, which illustrated (a) a tendency for compositional convergence along the drainage gradient after burning, (b) the divergence in composition between the two regions and (c) the general trend in

compositional variation between burnt and unburnt sites. The analysis underlines the importance of studying the effects of disturbance within the framework of variation along major environmental complex-gradients.

9.4 Conclusion

Indirect gradient analysis, based largely on the use of DCA, has proved to be a valuable approach to the understanding of the complex pattern of compositional variation in the subalpine and alpine vegetation of the Mt. Field Plateau. The analysis recognised two major directions of compositional variation, which were closely related to the altitude and drainage gradients used in the direct gradient analysis (Chapter 8).

Critics of indirect gradient analysis would probably argue that the overriding importance of the drainage and altitudinal gradients was apparent before ordination, and that the ordination has simply "restated the obvious". With respect to these two major complex-gradients, it would be more correct to say that the ordination has "confirmed and clarified the ostensible". The fact that the two major directions or trends in compositional variation extracted by the ordination were related to altitude and drainage, vindicates the choice of these two gradients as axes for direct gradient analysis. The ordinations confirmed that compositional variation along these two major gradients was essentially continuous. The frequent intermingling of quadrats with adjacent drainage scores, and the occasional placement of a quadrat with a given score among quadrats with scores several steps removed, suggests that the position of quadrats on the drainage gradient was not "obvious"

in the field. The ordination co-ordinates of quadrats may provide a more reliable indication of their position on the drainage gradient than could be obtained by direct environmental measurements. The same is true, though probably to a lesser extent, for the altitudinal gradient.

The indirect gradient analyses also revealed the existence of further compositional gradients which were not related to altitude or drainage. In the DCA ordination of the total data set, the fourth axis described a compositional gradient among subalpine forests on well drained soils, which has been tentatively related to firing history. The second axis of the DCA ordination of the upper alpine sub-set was apparently related to the duration of snow-lie. The elucidation of these trends in vegetational composition, which were not obvious before analysis, illustrates the heuristic value of ordination.

The present applications of DCA have demonstrated its utility in plant ecology, but also revealed some undesirable features of the method (or the program DECORANA), which require attention. The extraction of a spurious "interaction" axis before the interpretable "firing history" axis, does not support the contention of Hill and Gauch (1980), that such interaction axes are "unlikely to confuse the picture in practice" because their eigenvalues are "much less than those for significant non-spurious axes". The present result shows that interaction axes may have larger eigenvalues than relatively minor, but nevertheless interesting compositional gradients. If the spurious nature of such interaction axes is not recognised (e.g. by the examination of stereograms), effort may be wasted in futile attempts at interpretation. Worse still, if it is decided that the variation related to such an axis is "uninterpretable", it may be incorrectly assumed that subsequent,

"less important" axes must also be uninterpretable. Potentially interesting variation may consequently be overlooked.

The extraction of interaction axes could be prevented by detrending the third and subsequent axes in DECORANA with respect to pairs of previously extracted axes, considered simultaneously (Hill 1979a). For example, when deriving the third axis, the plane defined by axes 1 and 2 could be divided into cells, and the weighted mean of the trial scores on axis 3 adjusted to zero in each cell. Such a procedure should eliminate the possibility of third and subsequent axes bearing a strong systematic relationship to pairs of previous axes. However, it would not guarantee that the fourth and subsequent axes were not related to a combination of three previously extracted axes, considered simultaneously. Nevertheless, it seems much less likely that such higher order interaction axes would have eigenvalues sufficiently large to be inter-leaved with "real" axes. Another major limitation of the program DECORANA is that it extracts only four axes. Situations in which more than four interpretable gradients may exist are not difficult to imagine. Both the experiments with simulated data reported in Part 1 and the present analyses of field data have shown that the "reciprocal ordering" model of DCA can lead to distorted representations of underlying compositional gradients (e.g. Figures 4.4, 4.8, 4.9, 9.7, 9.8). Thus, although DCA may be regarded as one of the best currently available techniques for indirect gradient analysis, the speculation of Gauch (1982), that DCA may be close to an ideal "general purpose" ordination technique, seems premature.

CHAPTER 10 : CLASSIFICATION

10.1 Introduction

The results of direct and indirect gradient analyses have indicated that the subalpine and alpine vegetation of the Mt. Field Plateau forms a compositional continuum, with no marked discontinuities which might be used to delimit "natural types" of communities. Much of the compositional variation between sites may be understood in terms of the individualistic ecological response surfaces of species in relation to the altitudinal and drainage gradients. Although the vegetation pattern is perceived as essentially continuous, it was felt that dissection into a manageable number of classes would be useful for the purpose of synoptic description. The resulting classes or noda could then serve as arbitrary, but nevertheless convenient reference points within the continuum (cf. Poore 1962; Goodall 1963).

A large number of techniques for numerical classification have been developed since the early 1950's. Such methods are now widely used in vegetation studies. Recent reviews of the theory and practice of numerical classification in ecology have been provided by Orloci (1978a) and Goodall (1978).

10.2 Methods

The 398, 100m^2 quadrats which comprised the "total data set" for indirect gradient analysis (see section 9.2.1) were subjected to numerical classification by three hierarchical techniques, using integer cover class data for 139 species. The methods used were as follows:

(1) Two-way Indicator Species Analysis, using the program TWINSPAN (Hill 1979b). TWINSPAN is an updated version of the Indicator Species Analysis described by Hill, Bunce and Shaw (1975). It is a divisive, polythetic approach. A unidimensional Reciprocal Averaging (RA) ordination is first performed on the full set of quadrats and the quadrats are divided into two clusters by splitting the RA axis near its centre. Species whose frequency of occurrence differs markedly between the two groups are then identified as "indicator species" and the division is refined using the species with maximum indicator value. Within each of the resulting two clusters, the ordination and division process is repeated, to give four clusters. The entire procedure is repeated until the number of quadrats in each cluster falls below a chosen minimum value. The indicator species at each dichotomy provide a key to the hierarchical classification, which enables quadrats not included in the analysis to be subsequently keyed out into the most appropriate cluster. TWINSPAN also classifies the species, based on their frequencies of occurrence in each of the previously defined quadrat clusters. The quadrat and species classifications are then used in combination, to produce an ordered data matrix. TWINSPAN is apparently unique among hierarchical classification

programs, in that it pivots each dichotomy, in order to ensure, as far as possible, that adjacent clusters in the dendrogram are maximally similar.

(2) Average Linkage, alias the unweighted pair-group method using arithmetic averages (UPGMA) of Sokal and Michener (1958; see also Sneath and Sokal 1973). This is a polythetic, agglomerative technique, in which the similarity between two clusters is defined as the arithmetic average of the similarities between each pair of units, one from each cluster. The Average Linkage classification was performed using the CLUSTAN package (Wishart 1978), operating on a matrix of percentage similarity coefficients.

(3) Minimum Sum-of-Squares Clustering (Ward 1963; Orloci 1967), a polythetic, agglomerative technique which attempts to minimise the within-cluster sum-of-squares (i.e. the sum of the squared distances between each quadrat and the centroid of its cluster). The method is only applicable to Euclidean metrics. In the present case it was applied to a matrix of relativised Euclidean distances ("chord distance" of Orloci 1967, 1978a) between each pair of quadrats, using the CLUSTAN package (Wishart 1978). Minimum Sum-of-Squares Clustering proceeds by fusing, at each stage, that pair of clusters (or individual units) which causes the smallest increase in the within-cluster sum-of-squares. However, there is no guarantee that the sum-of-squares at a given stage during the fusion process is the minimum possible for that number of clusters. This is a consequence of the strictly hierarchical nature of the procedure. A number of methods have been proposed to optimise the within-cluster sum-of-squares, for a

specified number of clusters, by iteratively moving units between the clusters. In the present study, a technique similar to that of Jancey (1966) was employed for this purpose. The method was applied at each of several selected grouping levels. The computations were performed using the CLUSTAN package (Wishart 1978). For a given classification, the distance between each quadrat and the centroid of each existing group is calculated. In computing the distance between a quadrat and the centroid of the group of which it is currently a member, the quadrat is temporarily removed from that group. Each unit is then moved to its closest group and the centroids of the new groups are computed. The process is repeated until no relocation of quadrats occurs during a cycle.

The objective of classification in the present study was to provide an equitable dissection of the vegetational continuum, so as to facilitate synoptic description of the vegetation pattern. There appear to have been few studies of the relative efficiency of classificatory techniques for the dissection of continua. Gauch and Whittaker (1981) applied five methods, including the three employed in the present study, to data derived from Gaussian models and five sets of field data. They considered that TWINSPAN was generally the most successful method, although other techniques produced superior or complementary results in some cases. The present study did not attempt a detailed assessment of the relative performance of the three methods. Rather, the techniques were applied with the aim of producing alternative dissections of the continuum, from among which that solution considered most useful for descriptive purposes could be selected.

In dissecting a continuum, a decision concerning the number of clusters or groups to be recognised is essentially arbitrary, although the application of a "stopping rule" in some hierarchical procedures may give an impression of non-arbitrariness (cf. Goodall 1978). In the present case, a sufficient number of groups was required to ensure that the amount of compositional variation within groups was acceptably small. However, the desire to minimise within-group variability had to be balanced against the need to keep the number of groups low enough to provide a manageable system of reference classes.

Several computer programs were developed to assist in the evaluation and interpretation of clustering results. One program computed summary statistics for the species occurring in each cluster of a given classification. These included the mean percentage cover and its standard deviation, the frequency of occurrence in the cluster and pseudo t and G statistics. The t statistic was calculated as $(Mc-M)/\sqrt{(S/n)}$, where Mc is the mean abundance of the species in the cluster, M is the grand mean abundance in the total set of quadrats, S is the grand standard deviation and n is the number of quadrats in the cluster. The statistic was not intended for use in a probabilistic test. It simply provided a useful indication of the degree to which the cluster mean differed from the grand mean, making due allowance for the size of the cluster. Similarly, the G statistic was intended to express the degree to which the frequency of occurrence within a cluster differed from that in the remainder of the data set. The statistic was computed, as shown by Sokal and Rohlf (1969: pp.589-592), from the 2X2 contingency table defined by presence or absence of the species and

membership or non-membership of the cluster. G is equivalent to twice the "mutual information", as defined by Orloci (1978a: p.75).

Another program was designed to compute summary statistics for environmental variables and community characteristics for each cluster of a given classification. The statistics included the mean, standard deviation, minimum, maximum, 25,50 and 75 percentiles. Further programs were written to print ordered tables of the mean and frequency of selected species in each cluster of a given classification, and to plot cluster membership on an ordination. The latter was found to be a useful aid to the understanding of the multidimensional relationships between clusters and their distributions within the vegetational continuum.

In addition to the quadrat classifications, the 139 species included in the total data set were classified, in an attempt to delimit groups of species with similar patterns of occurrence and hence similar ecological propensities. Early approaches to the numerical classification of species (e.g. Williams and Lambert 1961) simply transposed the data matrix, and treated the species in the same manner as quadrats in a "normal" analysis. It was found that the resulting groups were often dominated by "frequency effects". Species with similar frequencies of occurrence in the data set tended to be grouped together, whether or not their patterns of occurrence were similar.

Austin and Belbin (1980, 1982) have developed an alternative approach to species classification, based on the notion that species association is best measured asymmetrically. Their method, which is known by the title TWO-STEP, is based on the computation of an

asymmetric measure of dissimilarity between each pair of species. This produces a matrix in which a given element, Dij, represents the dissimilarity of species i to species j. A symmetric matrix is then computed by pairwise comparison of the rows in the asymmetric matrix. An element, Tij, in this symmetric matrix expresses the degree to which species i and j share similar patterns of dissimilarity to each other species. The symmetric dissimilarity matrix may be subjected to hierarchical, agglomerative classification. For this purpose, the authors employed the flexible sorting strategy of Lance and Williams (1966), with beta= -0.25. In the terminology of Lance and Williams (1967), flexible clustering with beta= -0.25 is "space dilating". As a group increases in size during the fusion process, its apparent dissimilarity with other groups tends to increase. This prevents large groups from growing at the expense of smaller groups, and results in the formation of balanced, compact clusters. The symmetrical dissimilarity measure produced by TWO-STEP is also suitable for use with some other hierarchical sorting strategies, such as Average Linkage.

The 139 species included in the total data set were subjected to four classifications by the TWO-STEP procedure. Details of the data types and sorting strategies used were as follows:

(1) Unstandardised integer cover class data, with flexible sorting (beta= -0.25).

(2) Integer cover class data, standardised by species norm, with flexible sorting (beta= -0.25).

(3) Presence-absence data, with flexible sorting (beta= -0.25).

(4) Unstandardised integer cover class data, with the Average Linkage sorting strategy.

Austin and Belbin (1980, 1982) found that standardisation by species norm was sometimes advantageous for quantitative data, but they did not recommend the standardisation of qualitative (presence-absence) data. The TWO-STEP dissimilarity matrices were computed using an original FORTRAN program, and the CLUSTAN package (Wishart 1978) was then used for hierarchical fusion by the chosen strategy.

The results of the TWO-STEP species classifications were evaluated in the light of prior knowledge of the ecological distributions of species, as revealed by direct and indirect gradient analyses and extensive field observations. The multidimensional relationships among the species groups at selected levels in the hierarchy were studied by plotting class membership on the species ordinations produced by DCA of the total data set (see section 9.3.1). The TWO-STEP classifications were also compared with the species classifications produced by TWINSPAN.

Finally, selected quadrat and species classifications were combined, to produce two-way tables of mean cover and frequency of species within each quadrat group, or nodum. In these tables, the species were arranged in the groups defined by the species classification, and both noda and species groups were ordered in a manner reflecting their environmental relationships.

10.3 Results

10.3.1 Quadrat Classifications

Both TWINSPAN and Minimum Sum-of-Squares Clustering produced classifications in which the groups at any given level in the hierarchy represented a reasonably equitable dissection of the vegetational continuum. In contrast, the Average Linkage strategy resulted in unbalanced classifications, with a few large groups and many small groups, having only one or a few members. The method appeared to exaggerate the distinctiveness of individual quadrats, or small groups of highly similar quadrats, which occupied regions of locally lower density on the periphery of the continuum. Average Linkage is widely used in numerical taxonomy, where it is regarded as a good, general purpose method of classification (Sneath and Sokal 1973). The method is probably most successful with data sets containing "natural" groups, separated by relatively marked discontinuities. For the purpose of providing a balanced dissection of a continuum, Average Linkage appears to be unhelpful, and its results will not be considered further.

TWINSPAN tended to divide the quadrats in such a manner that the resulting groups occupied approximately equal volumes in the DCA ordination (cf. Gauch and Whittaker 1981). The distribution of the 16 group TWINSPAN classification (i.e. level 4 in the hierarchy, on the first two axes of the DCA ordination of the total data set (cover class data), is illustrated in Figure 10.1. This diagram shows the centroid of the quadrats in each cluster, and indicates the amount of scatter of individual quadrats within a cluster by means of a circle, whose radius is equal to the RMS average of the ordination distances between member

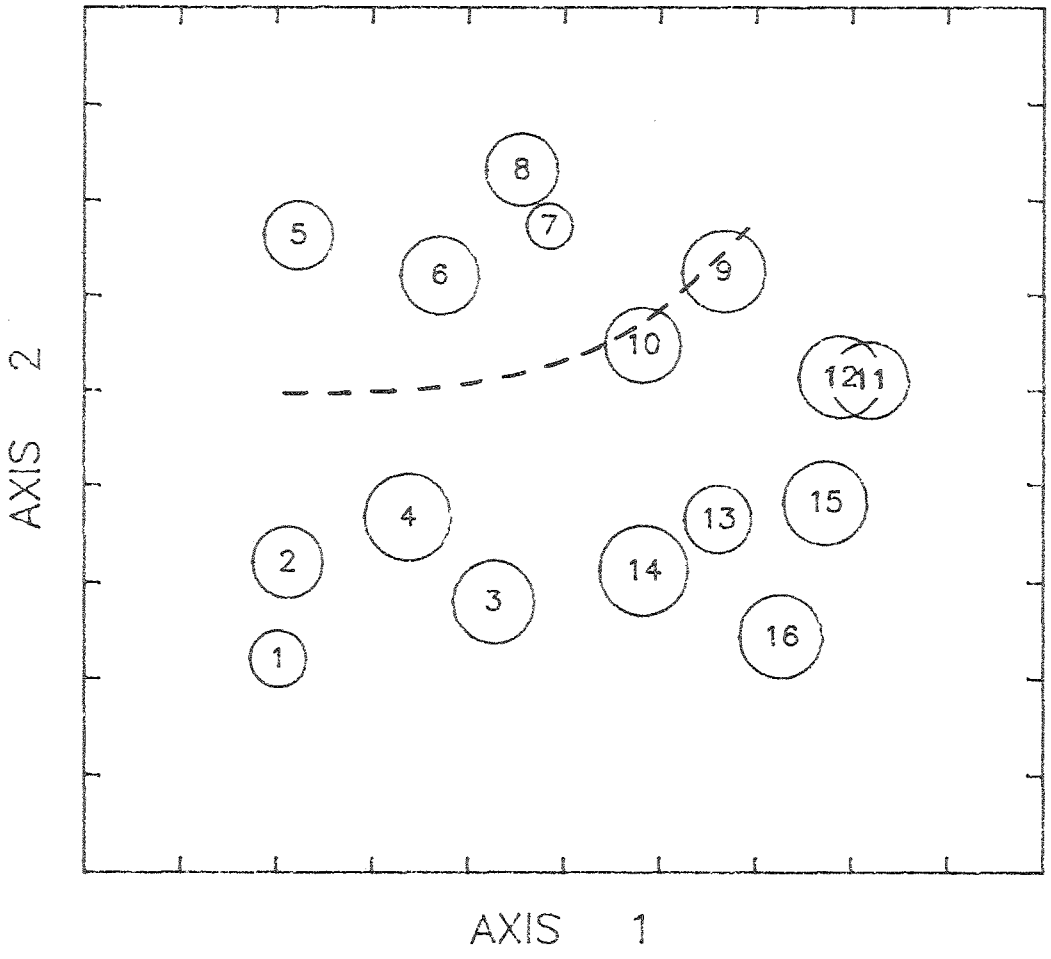


Figure 10.1 The disposition of the 16 quadrat groups, at level 4 in the hierarchy produced by TWINSPAN, on the first two axes of the DCA ordination of the total data set. The numbers are arbitrary group labels, marking the centroid of the co-ordinates of the quadrats in each group. The circle radii are equal to the RMS average of the ordination distances between individual member quadrats and the group centroid. The dashed line indicates the approximate location within the compositional continuum of the transition from subalpine to alpine vegetation at about 1220 m on the altitudinal gradient.

quadrats and the centroid. Groups 11 and 12 display considerable overlap in the two-dimensional ordination, but they are separated on the fourth, "firing history", axis. Group 12 comprises the rainforest/mixed forest quadrats at the lower extreme of axis 4. The approximate position of the transition from subalpine and alpine vegetation in the ordination is shown by a dashed line. This corresponds to an altitude of about 1220m. Although this 16 group classification may be regarded as a fairly equitable dissection of the continuum, it was considered unsatisfactory for two reasons. Firstly, groups 9 and 10 each included both subalpine woodland and alpine heath quadrats, since they straddled the transition between subalpine and alpine vegetation within the continuum. Secondly, the remainder of the alpine quadrats were divided into only four groups. The alpine quadrats occupy a smaller volume in the ordination than the subalpine quadrats, primarily because of the decrease in beta diversity along the drainage gradient towards higher elevations (see section 8.2.3.4). The four alpine groups were unacceptably heterogeneous in terms of their vegetation. Each contained quadrats from a relatively broad segment of the drainage gradient.

An examination of the 31 group TWINSPAN classification (level 5 in the hierarchy) revealed a more acceptable partitioning of the alpine quadrats. In addition, the groups which straddled the alpine-subalpine boundary were each divided into an alpine and a subalpine group at level 5. However, the subalpine quadrats were now divided into an inconveniently large number of groups, many of which contained less than 10 quadrats. It was considered that a system of 31 classes would be too unwieldy for the purpose of synoptic description. A possible solution to this problem is to accept only those divisions at level 5 which

operate among alpine quadrats. Such a procedure produces 22 groups. However, this classification will not be considered in detail, since the Minimum Sum-of-Squares Clustering solution at a similar grouping level was considered superior.

The hierarchy produced by Minimum Sum-of-Squares Clustering was intercepted at the 30, 25, 20 and 15 group levels and the resulting classifications were examined. The 20 group solution appeared to provide a fairly equitable dissection of the continuum. However, one large group of alpine quadrats was regarded as unacceptably heterogeneous. It was found that this group was the next to divide in the hierarchy. Consequently, the 21 group solution was adopted as a working classification. Iterative relocation of the 21 group classification resulted in a modest reduction in the within-group sum-of-squares, from 118.3 to 115.6.

The mean values of environmental variables and community characteristics in each of the 21 optimised groups or noda are given in Table 10.1. Figure 10.2 illustrates the distribution of the 21 noda on axes 1 and 2 of the DCA ordination of the total data set (cover class data). The classification dissects the continuum in an equitable manner, with approximately equal emphasis on the alpine and subalpine vegetation. The former is divided into nine groups and the latter into twelve.

The disposition of the groups on the DCA ordination (Figure 10.2) suggests that the compositional variation between groups may be largely explained in terms of vegetational response to the altitudinal and drainage gradients. Mean altitudes and drainage scores for the quadrats

	NODUM																				
	14	3	19	17	6	15	5	12	16	11	20	18	13	2	10	9	7	1	4	8	21
NUMBER OF QUADRATS	21	31	20	15	24	24	14	24	21	12	6	18	18	35	22	18	13	12	24	19	7
ALTITUDE (m)	1026	1090	1198	1263	985	1038	1062	1235	1245	1293	1007	1076	1046	1142	1238	1318	1040	1095	1174	1259	1368
DRAINAGE SCORE	1.3	1.3	2.6	1.1	2.9	2.9	2.9	3.2	3.0	3.0	4.2	4.0	4.1	4.1	4.0	3.9	5.0	4.9	4.9	4.7	5.0
ANNUAL RADIATION (Kj/sq.cm)	15.0	15.2	15.1	15.0	15.1	14.8	14.8	14.9	15.1	15.2	10.8	14.9	14.9	15.1	15.2	14.4	15.1	14.4	15.4	15.4	15.1
SLOPE (degrees)	4	4	12	2	13	8	8	10	10	4	33	11	14	6	11	16	9	13	12	9	4
ROCK COVER (%)	5	3	30	7	10	24	19	30	18	17	51	54	52	56	62	48	85	80	81	80	85
WIND EXPOSURE *	2.6	2.7	3.0	4.0	1.1	1.9	1.9	3.4	3.3	3.9	1.0	1.6	2.1	2.3	3.4	3.2	1.2	1.3	2.6	3.3	4.0
HT. OF TALLEST STRATUM (m)	0.9	1.0	0.8	0.4	13.7	10.2	5.8	0.8	1.4	0.5	10.3	15.4	12.4	8.5	0.7	0.7	15.0	15.3	6.7	0.4	0.3
TOTAL COVER (%)	149	157	99	116	209	192	162	99	117	116	145	157	165	134	105	102	122	125	112	69	24
PERCENTAGE DOMINANCE	49	54	41	48	49	53	48	45	57	44	47	51	50	48	47	58	55	46	46	37	72
SIMPSON'S INDEX	0.18	0.21	0.13	0.17	0.18	0.19	0.18	0.17	0.24	0.16	0.17	0.18	0.17	0.17	0.17	0.24	0.24	0.18	0.18	0.15	0.42
ALPHA DIVERSITY (total)	23.6	23.3	32.7	32.4	22.2	25.8	27.9	28.2	28.3	24.8	24.8	25.8	25.9	24.9	26.8	19.3	23.7	26.1	21.3	19.1	10.9
No. of trees	0.7	0.3	0.4	0.0	4.9	3.4	2.0	0.5	0.5	0.0	4.8	3.7	3.4	1.2	0.1	0.2	2.9	3.1	1.1	0.2	0.0
No. of erect shrubs	7.3	7.8	13.1	8.5	11.3	11.0	11.1	12.3	12.9	8.3	12.8	13.0	13.3	13.9	12.6	9.7	11.0	11.3	12.0	12.7	5.3
No. of prostrate shrubs	0.1	0.4	2.5	3.3	0.2	0.4	0.4	1.8	2.4	2.8	0.2	0.3	1.6	1.0	2.1	1.3	0.2	0.5	0.9	0.8	0.1
NO. OF WOODY SPECIES	8.1	8.5	16.0	11.8	16.4	14.8	13.5	14.6	15.8	11.1	17.8	17.0	18.3	16.1	14.8	11.2	14.1	14.9	14.0	13.7	5.4
No. of graminoids	9.5	8.8	8.7	9.1	3.8	6.9	7.8	6.7	6.8	6.8	1.8	3.4	3.9	4.6	5.7	4.1	3.5	4.3	3.6	3.4	2.4
No. of perennial herbs	4.0	4.3	6.0	8.9	1.6	3.1	4.6	5.4	4.3	4.7	3.5	4.5	3.3	3.5	4.9	2.6	4.8	5.8	3.0	1.5	2.6
No. of annuals/geophytes	0.9	0.6	1.2	1.7	0.1	0.5	0.5	0.5	0.5	0.9	0.2	0.0	0.0	0.0	0.1	0.6	0.0	0.0	0.0	0.1	0.1
No. of ferns/lycopsids	1.1	1.1	0.8	0.9	0.3	0.5	1.5	1.0	0.9	1.3	1.5	0.9	0.4	0.7	1.3	0.8	1.3	1.1	0.7	0.4	0.3
NO. OF NON-WOODY SPECIES	15.5	14.8	16.7	20.6	5.8	11.0	14.4	13.6	12.5	13.7	7.0	8.8	7.6	8.8	12.0	8.1	9.6	11.2	7.3	5.4	5.4
"RAINFOREST INDEX"	0.0	0.0	2.4	0.0	15.7	5.4	0.7	2.3	5.2	0.0	80.1	31.0	3.5	2.3	1.2	2.8	14.4	44.3	12.4	3.6	0.0
"CONIFER INDEX"	0.6	1.6	21.5	33.6	0.1	0.0	2.3	7.5	54.5	26.7	5.2	0.4	0.0	2.6	8.6	14.7	0.9	0.7	8.7	11.3	4.4

* Wind exposure was assessed on a four point relative scale : 1=low, 2=moderate, 3=high, 4=extreme.

TABLE 10.1 Mean values of environmental variables and community characteristics in each of the 21 noda produced by Minimum Sum-of-Squares Clustering of the total data set (cover class data), followed by iterative relocation. The noda have been arranged in four series, according to their mean drainage scores, and ordered by mean altitude within each series. For details of the calculation of the "rainforest index" and the "conifer index", see the text.

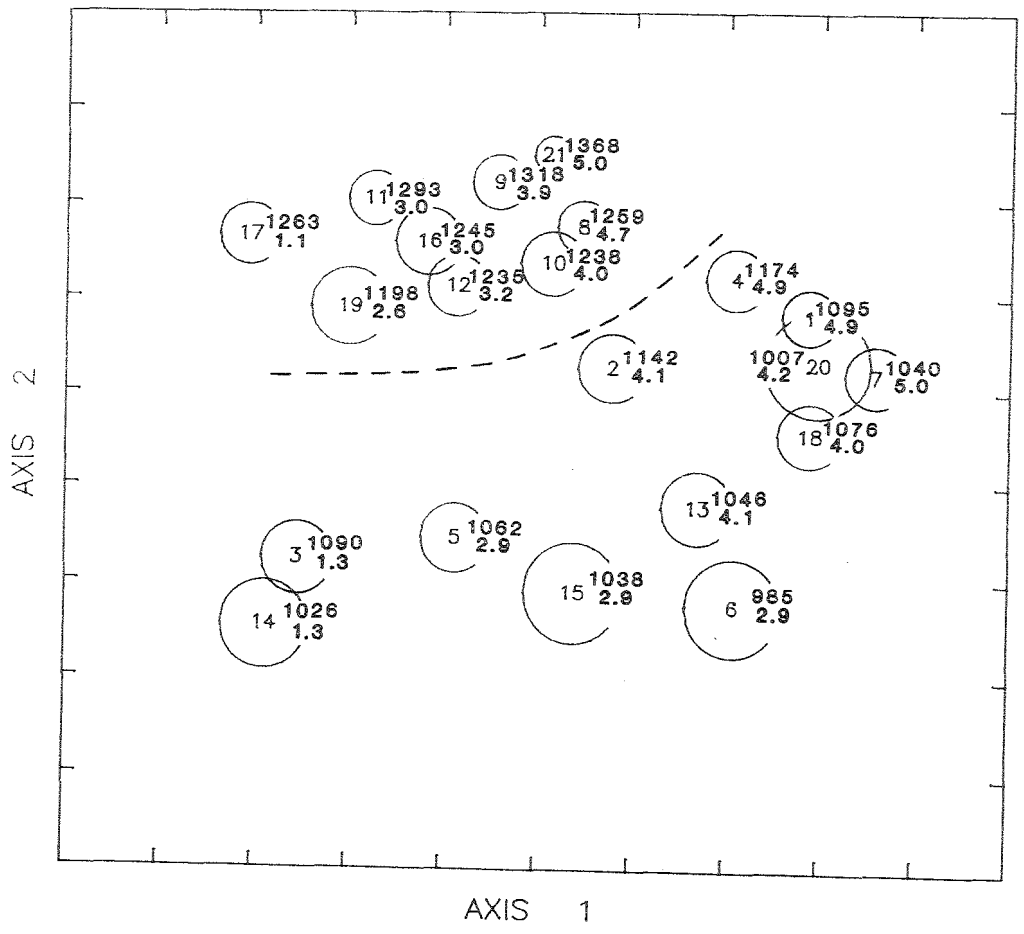


Figure 10.2 The disposition of the 21 optimised Minimum Sum-of-Squares classificatory groups with respect to the first two axes of the DCA ordination of the total data set. The numbers at the centre of the circles are arbitrary group labels, marking the centroids of the co-ordinates of the quadrats in each group. The circle radii are equal to the RMS average of the ordination distances between individual member quadrats and the group centroid. Adjacent to each group centroid, the mean altitude (top figure) and mean drainage score (bottom figure) of the quadrats comprising that group are given. The dashed line indicates the approximate location within the compositional continuum of the transition from subalpine to alpine vegetation, at about 1220 m on the altitudinal gradient.

in each group (Table 10.1; see also Figure 10.2) are largely in accordance with such an interpretation. However, the positions of some groups within the two-dimensional ordination are somewhat anomalous in this respect.

Group 20 appears to overlap with groups 1, 4, 7 and 18, but it is clearly separated from them on the fourth ordination axis (Figure 10.3). Axis 4 has been tentatively related to firing history (see section 9.3.1), and group 20 comprises those quadrats with extremely low scores on axis 4. Such quadrats were in fire-protected locations and carried temperate rainforest or mixed forest. The position of group 20 relative to groups 7 and 18 on the two-dimensional ordination is inconsistent with its lower mean altitude.

The direction of separation of groups 13 and 18 in the two-dimensional ordination suggests a difference in drainage, with group 18 being better drained. However, the mean drainage scores for these two groups are very similar (Table 10.1). The position of group 6, relative to group 15, is consistent with the lower mean altitude of group 6. However, it implies a relative improvement in drainage conditions in group 6 which is not supported by the mean drainage scores. These apparent inconsistencies may be partly attributable to the crudeness of the drainage scores as indices of position on the drainage gradient. However, an examination of the positions of the groups on axis 4 of the ordination (Figure 10.3) suggested an alternative explanation. Groups 6 and 18 have lower mean scores on axis 4 than groups 13 and 15, indicating a tendency towards the rainforest/mixed forest composition typified by group 20. The anomalous

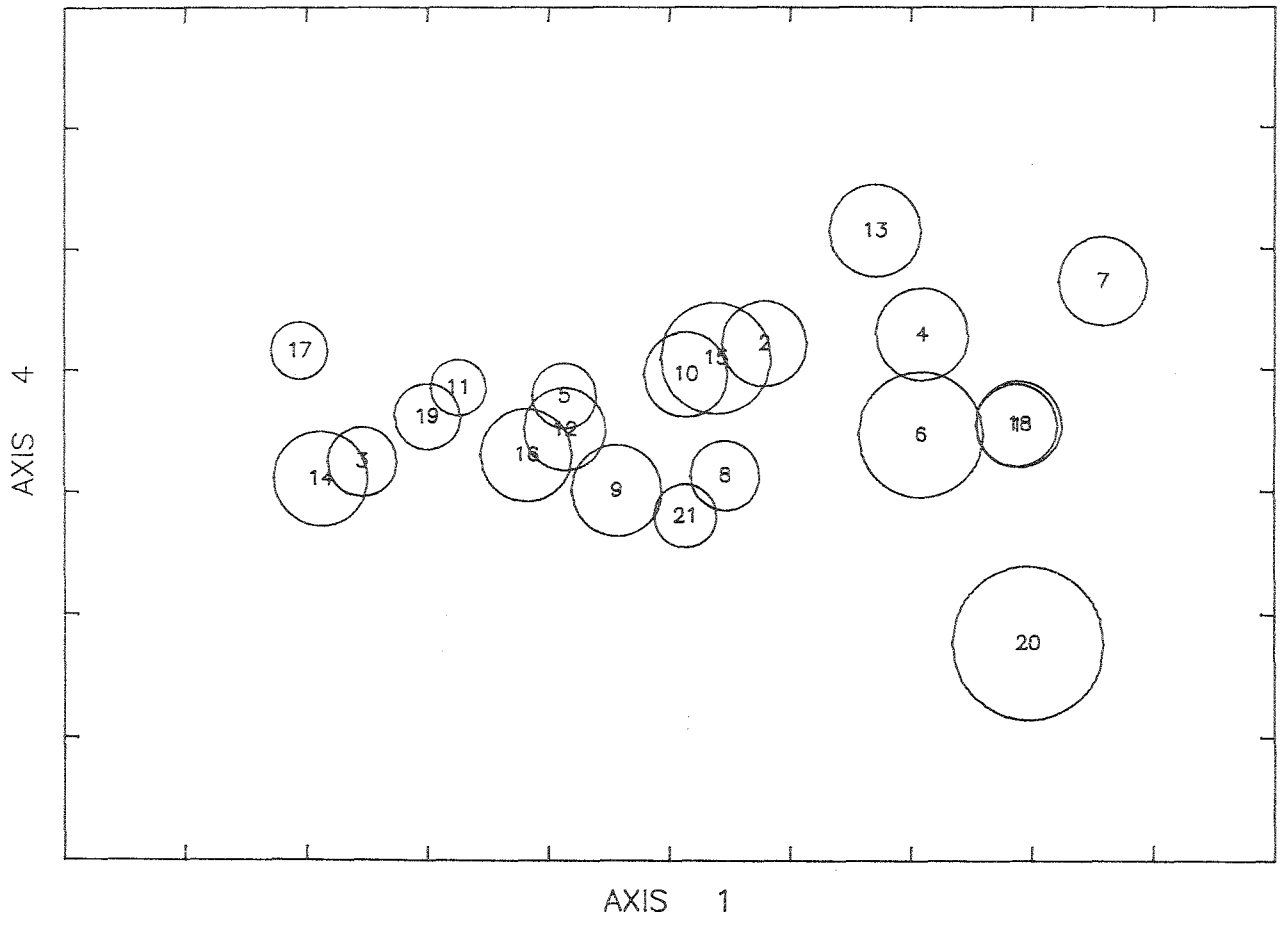


Figure 10.3 The disposition of the 21 optimised Minimum Sum-of-Squares classificatory groups with respect to axes 1 and 4 of the DCA ordination of the total data set. Adjacent to the centroid of each forest group, the value of the "rainforest index" (the sum of the mean percentage covers of the rainforest species occurring in that group) is indicated.

positions of groups 6 and 18 on axes 1 and 2 of the ordination may therefore reflect a partial confounding of variation along the "firing history" gradient with variation on the two major gradients.

In an attempt to quantify the positions of the groups on the "firing history" compositional gradient, a "rainforest index" was defined, as the sum of the mean percentage cover values in a group of those species listed by Jarman and Brown (1983: Table 1) as rainforest species. Species listed therein as "doubtful" rainforest species were excluded from the calculations, as were the shrubs Coprosma nitida and Drimys lanceolata, which are widespread generalists at Mt. Field. The resulting "rainforest index" values are given in Table 10.1. The distribution of the values with respect to axes 1, 2 and 4 of the DCA ordination is indicated in Figure 10.4. The marked relationship between axis 4 and the "rainforest index" is obvious (Figure 10.4b), as is the tendency for groups with high index values to be displaced towards group 20 on the first two axes (Figure 10.4a).

The partial confounding of "firing history" variation on the first two DCA axes was not appreciated when interpreting the ordination results. Classification of the quadrats into a relatively small number of groups facilitated the recognition of this phenomenon, by reducing the number of comparisons to a manageable level. This is one illustration of the complementary roles of ordination and classification.

Groups 12 and 16 overlap on the first two axes of the DCA ordination (Figure 10.2) and their mean altitudes and drainage scores are very similar (Table 10.1). Furthermore, they are not separated on

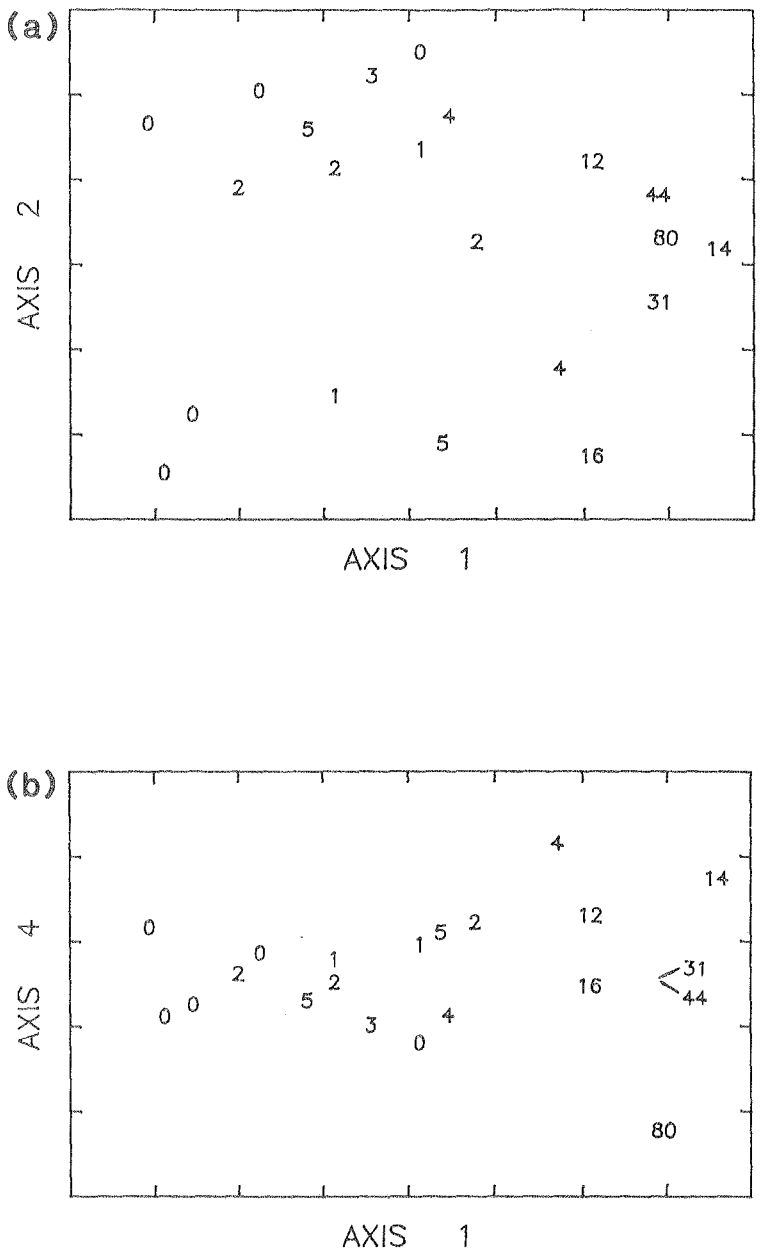


Figure 10.4 The distribution of "rainforest index" values for each of the 21 Minimum Sum-of-Squares quadrat groups, with respect to (a) axes 1 v. 2 and (b) axes 1 v. 4 of the DCA ordination of the total data set. The index value for a group is the sum of the mean percentage covers of those rainforest species which occur in that group. For each group, the value is plotted at the centroid of the ordination co-ordinates of its individual member quadrats.

axis 4 of the ordination (Figure 10.3). A comparison of the mean cover and frequency of species in these two groups, revealed relatively few floristic differences. The major reason for the separation of the groups in the classification appears to be the greater frequency and mean cover of the conifers Athrotaxis cupressoides, Diselma archeri, Microcachrys tetragona, Microstrobos niphophilus and Podocarpus lawrencii in group 16. These conifers are known to be eliminated, or severely reduced in abundance, by fire (Jackson 1973; Kirkpatrick, Dickinson and Cantle 1982; Kirkpatrick 1983; see also section 9.3.8).

A "conifer index" was defined as the sum of the mean percentage cover values in a group, of the conifer species listed above. The index values for each nodum are given in Table 10.1. Group 16 has the highest value (54.4%), while group 12 has one of the lowest (7.5%). It is postulated that the compositional variation between groups 16 and 12 is primarily related to an underlying difference in firing frequency, or the length of time since the last fire. Of the 21 quadrats in group 16, 16 carry closed coniferous heaths, with a percentage cover of conifers greater than 70%. Such heaths probably require a fire-free period of at least 200 years for development. The conifers have extremely slow growth rates (Ogden 1978). Some preliminary ring counts of Microstrobos niphophilus and Diselma archeri stems with diameters of 3-6cm, in heaths on Mawson Plateau, suggested ages of 250-300+ years.

This compositional gradient, among moderately drained sites between 1200 and 1300m in altitude, was not identified in the indirect gradient analyses. A re-examination of the DCA ordination of the lower alpine subset, revealed a tendency for quadrats in group 16 to be separated from those in group 12 on the second axis. However, axis 2

confounded the supposed "firing history" variation with compositional variation related to altitude.

10.3.2 Species Classifications

The species classification produced by TWINSPAN was considered markedly inferior to the TWO-STEP classifications. It will not be described in detail. Of the TWO-STEP classifications, the quantitative analysis based on Average Linkage was unsatisfactory. It produced a poorly structured hierarchy which permitted the recognition of relatively few groups, most of which were large and heterogeneous. Both the direct gradient analysis reported in Chapter 8, and species ordinations produced by DCA, indicated that species are individualistically distributed, with modes apparently scattered at random over the altitude X drainage ecoplane. Given that species do not form distinct groups with highly similar distributions, the most that can be expected of a species classification is that it arbitrarily divides the species into groups with relatively similar ecological distributions. Average Linkage, with its "space conserving" behaviour (Lance and Williams 1967), appears to be incapable of forcibly dissecting a relatively continuous configuration into equitable subsets. As noted in discussing the Average Linkage quadrat classification (section 10.3.1), the strategy seems to place too much emphasis on local structure.

The three TWO-STEP classifications employing flexible sorting were more successful. Flexible clustering with beta= -0.25 is "space dilating" (Lance and Williams 1967), and this seems to ensure a relatively equitable dissection of continua (see section 10.3.1 The

quantitative classification employing cover class data, normalised by species, was considered somewhat superior to the qualitative (presence-absence) classification. Both of these classifications were a marked improvement on the unstandardised, quantitative solution.

The normalised quantitative classification, at the 20 group level, is presented in Table 10.2. The analysis showed no tendency to be dominated by species abundance or presence: species with quite different frequencies of occurrence and mean cover were often grouped together. Most of the groups had relatively clear ecological interpretations. However, field experience and the results of direct gradient analyses suggested that a few species would be better placed in a different group. For example, Celmisia saxifraga, which was placed in group 2 (herbs of sporadic occurrence in non-forest communities), could justifiably be moved to group 16 (species of poorly drained to well drained alpine sites), since it is confined to the alpine zone. Such minor "misclassifications" are not considered a fault of the TWO-STEP technique. A degree of arbitrariness must be expected in the placement of "borderline" units whenever an essentially continuous population is dissected. Group 7 is a splinter group containing two species with widespread but sporadic distributions. These could be lumped with group 6.

The only really unsatisfactory group is group 12, which combines species with quite different ecological tolerances. Of the nine species originally included in group 12, Brachycome tenuiscapa and Campylaema lineare were considered better placed in group 11, Carex appressa and Centrolepis monogyna in group 1, Eucalyptus urnigera in group 10 and

GROUP 1 (N= 9) Species of poorly drained and waterlogged alpine sites (i.e. above 1200m).

Abrotanella forsteroides	21	Abrotanella scapigera	6	Actinotus suffocata	18
Carpha sp. nov.	16	Diplaspis cordifolia	21	Dracophyllum minimum	6
Ewartia meridithae	15	Mitrasacme archeri	29	Pterygopappus lawrencii	17

GROUP 2 (N= 5) Herbs of sporadic occurrence in non-forest communities.

Acaena montana	31	Celmisia saxifraga	30	Craspedia alpina	31
Euphrasia gibbsiae	37	Ewartia planchonii	22		

GROUP 3 (N=11) Species of well drained sites and boulderfields at altitudes less than 1050m (mostly rainforest species).

Acaena novae-zelandiae	12	Aristotelia peduncularis	26	Atherosperma moschatum	12
Athrotaxis selaginoides	7	Blechnum wattsii	5	Cyathodes glauca	26
Eucryphia milliganii	12	Olearia persoonioides	14	Phyllocladus asplenifolius	8
Pittosporum bicolor	15	Viola hederacea	16		

GROUP 4 (N= 8) Species of sporadic occurrence on well drained sites and boulderfields at all altitudes.

Agrostis parviflora	10	Blechnum penna-marina	17	Epilobium sarmentaceum	6
Grammitis armstrongii	24	Helichrysum ledifolium	18	Lissanthe montana	23
Luzula australasica ssp. australasica	22	Plantago tasmanica	30		

GROUP 5 (N= 5) Species of boulderfields and screes at altitudes greater than 1300m.

Archeria serpyllifolia	43	Cheesemannia radicata	5	Epilobium gunnianum	10
Gaultheria depressa	10	Ourisia integrifolia	9		

GROUP 6 (N=14) Widespread generalists, tending to be more frequent under moderately drained to waterlogged conditions.

Astelia alpina	326	Bellendena montana	110	Celmisia longifolia	191
Epacris serpyllifolia	268	Leptospermum rupestre	107	Lycopodium fastigiatum	92
Lycopodium scariosum	53	Mitrasacme montana	48	Orites acicularis	202
Pentachondra pumila	140	Pimelea sericea	58	Poa gunnii	257
Richea scoparia	176	Uncinia compacta	273		

GROUP 7 (N= 2) Species of widespread, but sporadic occurrence (could be fused with group 6).

Athrotaxis cupressoides	13	Lycopodium australianum	32

TABLE 10.2 The 20 group species classification produced by flexible clustering (beta=-0.25) of the TWO-STEP dissimilarity matrix, computed from cover class data, normalised by species. Adjacent to each species, its frequency of occurrence among the 398 quadrats of the total data set is given. There is no apparent tendency for the classification to be dominated by species frequency. Species with markedly different frequencies are often placed in the same group.

GROUP 8 (N= 5) Species of poorly drained to waterlogged sites at altitudes up to 1250m.

Baeckea gunniana	106	Empodisma minus	192	Scirpus aucklandicus	52
Senecio pectinatus var. pectinatus	58	Sprengelia incarnata	73		

GROUP 9 (N= 6) Species of moderate to well drained sites at altitudes less than 1050m.

Banksia marginata	20	Billardiera longiflora	5	Blandfordia punicea	8
Leptospermum nitidum	6	Monotoca submutica var. autumnalis	5	Pimelea drupacea	6

GROUP 10 (N= 7) Species of moderate to well drained sites at altitudes up to 1150m.

Bauera rubioides	179	Gahnia grandis	48	Hakea lissosperma	38
Leptospermum lanigerum	112	Lomatia polymorpha	55	Monotoca empetrifolia	47
Olearia erubescens	51				

GROUP 11 (N= 8) Species of poorly drained to waterlogged sites at altitudes up to 1150m.

Boronia citriodora	86	Diplarrena latifolia	95	Gleichenia alpina	85
Hakea epiglottis	39	Helichrysum hookeri	41	Lepidosperma filiforme	66
Oreobolus oxycarpus	48	Restio australis	36		

GROUP 12 (N= 9) Heterogeneous group (see text).

Brachycome tenuiscapa	18	Campynema lineare	19	Carex appressa	11
Centrolepis monogyna	20	Eucalyptus urnigera	23	Gymnoshoenus sphaerocephalus	6
Melaleuca squamea	15	Restio complanatus	16	Richea gunnii	14

GROUP 13 (N= 7) Species of well drained sites and boulderfields at altitudes up to 1100m.

Cardamine heterophylla	37	Geranium potentilloides	50	Nothofagus cunninghamii	45
Oxalis lactea	32	Polystichum proliferum	29	Richea pandanifolia	40
Senecio leptocarpus	29				

GROUP 14 (N= 8) Species of poorly drained to waterlogged sites at all altitudes, and moderately drained sites above 1200m.

Carpha alpina	163	Danthonia pauciflora	47	Drosera arcturi	56
Erigeron pappochroma	123	Euphrasia striata	90	Gentianella diemensis	81
Microstrobos niphophilus	98	Oreobolus pumilio	84		

TABLE 10.2 (Continued) The 20 group TWO-STEP species classification.

GROUP 15 (N= 7) Widespread generalists, tending to be more frequent on well drained sites and boulderfields.

Coprosma nitida	262	Drimys lanceolata	284	Exocarpos humifusus	149
Gonocarpus serpyllifolius	181	Orites revoluta	274	Richea sprengelioides	250
Rubus gunnianus	216				

GROUP 16 (N= 5) Species of poorly drained to well drained alpine sites (i.e. above 1200m).

Cyathodes dealbata	58	Diselma archeri	60	Erigeron stellatus	71
Microcachrys tetragona	64	Oreobolus acutifolius	76		

GROUP 17 (N= 6) Species of moderate to well drained sites and boulderfields at altitudes up to 1200m.

Cyathodes parvifolia	143	Eucalyptus coccifera	168	Eucalyptus subcrenulata	66
Gaultheria hispida	58	Orites diversifolia	72	Telopea truncata	104

GROUP 18 (N= 6) Species of well drained sites and boulderfields at altitudes above 1100m.

Cyathodes petiolaris	51	Danthonia fortuna-hibernae	92	Helichrysum backhousii	171
Hierochloe redolens	181	Olearia ledifolia	182	Podocarpus lawrencii	112

GROUP 19 (N= 7) Species of boulderfields and well drained sites at altitudes up to 1250m.

Cyathodes straminea	149	Deyeuxia monticola	109	Lagenophora stipitata	79
Olearia phlogopappa	70	Olearia pinifolia	98	Trochocarpa cunninghamii	106
Trochocarpa thymifolia	88				

GROUP 20 (N= 4) Species largely confined to the Tarn Shelf area.

Dracophyllum milliganii	7	Helichrysum pumilum	15	Lepidosperma lineare var. inops	15
Persoonia gunnii	22				

TABLE 10.2 (Continued) The 20 group TWO-STEP species classification.

Richea gunnii in group 8. The remaining three species formed an acceptable group, being largely confined to poorly drained and waterlogged sites below 1000m in altitude. Examination of the dendrogram showed that these three species fused at a relatively low level. The species included in group 12 were all of low frequency (occurring in less than 6% of the quadrats). The reason for their fusion at the 20 group level in the normalised classification is not clear. These 12 species were not combined at the 20 group level in the unstandardised quantitative classification.

Despite these minor aberrations, the 20 group TWO-STEP classification, based on normalised cover class data, was regarded as a useful summary of the ecological relationships of the species. The distribution of the 20 groups on the first two axes of the species ordination produced by DCA of the total data set (cover class data) is shown in Figure 10.5. Although the component species of most groups occupy relatively localised regions on the ordination, some groups overlap broadly. Perfect agreement between the TWO-STEP classification and the DCA ordination is not to be expected. The ordination represents the modal, or average positions of species. However, TWO-STEP groups species according to the overall similarity of their distributions, rather than simply combining species with co-incident modes. Nevertheless, the high dispersion of group 12 and the intermediate position of its centroid relative to groups 8, 10 and 11 accords with previous comments. The central positions of the "generalist" groups (6, 7 and 15) is also notable.

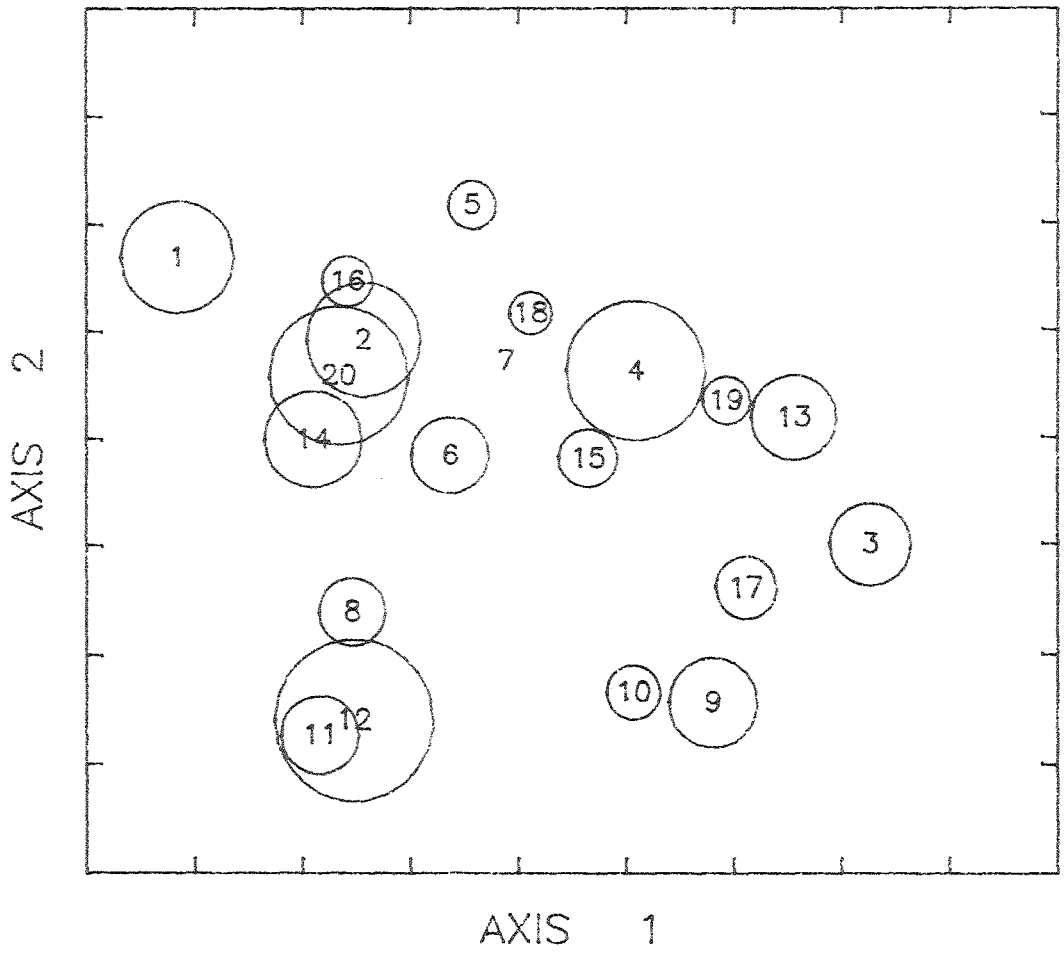


Figure 10.5 The disposition of the 20 species groups, produced by flexible sorting (beta = -0.25) of the TWO-STEP dissimilarity coefficient (calculated from cover class data, normalised by species), on the first two axes of the DCA species ordination of the total data set. The numbers at the centre of each circle are arbitrary group labels, which mark the centroid of the co-ordinates of the species in that group. The radii of the circles are equal to the RMS average of the ordination distances between individual member species and the group centroid.

10.3.3 Descriptions of Noda

Mean percentage cover and frequency of occurrence were computed for each species within each of the 21 quadrat groups of the relocated Minumum Sum-of-Squares classification, described in section 10.3.1. In the resulting tables, the quadrat groups, or noda were arranged into four series, according to their mean drainage scores, and within each series they were sorted in order of increasing mean altitude. The species were then arranged into groups, largely in accordance with the 20 group, normalised TWO-STEP classification, but with some manual relocation of species. The species groups were subsequently ordered, so as to concentrate the non-zero entries in the tables into the positive diagonal within each drainage series, as far as it was possible to do so. The resulting ordered two-way tables of mean cover and frequency are presented as Tables 10.3 and 10.4, respectively. These tables provide a powerful summary of the patterns of compositional variation on the Mt. Field Plateau. The variation among noda is largely related to the two major complex-gradients of drainage and altitude, with some differences between noda which occupy similar positions on these gradients having been attributed to firing history. The communities typified by each nodum, and their associated habitat conditions shall now be described.

Each nodum has been named after its "constant dominants". These are species with a mean percentage cover in the nodum of at least 10% and a frequency of occurrence of at least 90%. Where more than three species fulfilled these requirements, the three with highest mean cover were selected. The constant dominants are not necessarily good

	NODUM																				
	14	3	19	17	6	15	5	12	16	11	20	18	13	2	10	9	7	1	4	8	21
NUMBER OF QUADRATS	21	31	20	15	24	24	14	24	21	12	6	18	18	35	22	18	13	12	24	19	7
MEAN ALTITUDE (m)	1026	1090	1198	1263	985	1038	1062	1235	1245	1293	1007	1076	1046	1142	1238	1318	1040	1095	1174	1259	1368
MEAN DRAINAGE SCORE	1.3	1.3	2.6	1.1	2.9	2.9	2.9	3.2	3.0	3.0	4.2	4.0	4.1	4.1	4.0	3.9	5.0	4.9	4.9	4.7	5.0
Baeckea gunniana	5.7	7.3	2.3	0.8	+	1.2	3.3	0.7	1.0	-	-	-	+	0.2	-	-	-	-	-	-	-
Empodisma minus	11.1	9.9	6.3	10.3	10.1	13.4	9.6	1.5	0.3	1.7	-	+	1.6	1.3	-	-	+	-	+	-	-
Richea gunnii	0.3	0.4	-	1.3	0.8	0.2	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scirpus aucklandicus	+	0.1	+	+	+	+	0.1	+	0.1	0.1	-	-	+	+	+	+	-	-	-	-	-
Sprengelia incarnata	3.9	0.8	1.1	0.5	0.1	+	0.1	+	+	-	-	-	-	-	+	-	-	-	-	-	-
Senecio pectinatus var. pectinatus	+	+	+	+	-	+	+	+	+	+	-	-	+	+	+	+	-	-	-	-	-
Carpha alpina	4.5	1.8	2.7	9.4	+	1.0	0.5	1.4	1.3	2.5	-	+	-	+	0.3	+	-	+	-	+	-
Danthonia pauciflora	+	+	0.2	0.5	-	-	-	+	+	0.1	-	-	-	-	-	+	-	-	-	-	-
Drosera arcturi	0.3	+	0.2	0.2	+	+	+	+	0.3	-	-	-	-	-	-	+	-	-	-	-	-
Erigeron pappochroma	0.1	0.3	+	0.1	+	+	0.1	0.1	+	+	-	-	-	+	+	0.1	-	+	-	+	+
Euphrasia striata	+	+	0.2	0.1	+	+	+	0.1	+	+	0.1	+	+	+	0.1	-	-	-	-	-	-
Gentianella diemensis	+	+	+	+	-	+	+	+	+	+	-	-	-	+	+	+	-	-	-	+	+
Microstrobos niphophilus	0.6	1.6	12.3	22.8	-	-	2.3	6.3	29.4	0.5	-	-	-	0.8	0.5	-	-	-	-	0.3	-
Oreobolus pumilio	1.4	0.6	5.1	3.5	-	+	0.1	0.2	1.1	0.1	-	-	-	-	+	+	-	-	-	-	-
Banksia marginata	-	-	-	-	12.2	0.5	-	-	-	-	-	-	1.7	-	-	-	-	-	-	-	-
Billardiera longiflora	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-
Blandfordia punicea	-	-	+	-	-	-	-	-	-	-	-	-	0.4	+	-	-	-	-	-	-	-
Leptospermum nitidum	+	-	-	-	0.5	-	-	-	-	-	-	1.1	-	-	-	-	-	-	-	-	-
Pimelea drupacea	-	-	-	-	+	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	-
Monotoca submutica var. autumnalis	-	-	-	-	+	-	-	-	-	-	-	-	2.3	-	-	-	-	-	-	-	-
Bauera rubioides	6.7	1.2	5.2	-	54.8	53.3	28.3	0.9	-	-	-	37.9	34.8	21.9	-	-	10.5	-	4.5	-	-
Eucalyptus subcrenulata	-	0.6	-	-	29.9	1.8	1.9	-	-	-	12.6	8.8	4.4	1.4	-	-	11.6	1.7	-	-	-
Eucalyptus urnigera	-	+	-	-	0.3	7.1	0.4	-	-	-	-	0.3	0.3	-	-	-	-	-	-	-	-
Gahnia grandis	-	+	-	-	9.8	1.9	0.1	-	-	-	-	+	0.4	-	-	-	+	-	+	-	-
Hakea lissosperma	-	-	-	-	2.4	1.4	0.4	-	-	-	-	0.3	7.8	-	-	-	-	-	-	-	-
Leptospermum lanigerum	6.9	2.8	-	-	28.1	46.3	21.9	-	-	-	0.1	13.2	8.3	0.5	-	-	0.5	0.5	0.3	-	-
Lomatia polymorpha	0.1	-	0.3	-	1.0	1.2	0.1	-	-	-	-	0.1	0.8	0.5	-	-	-	-	-	-	-
Monotoca empetrifolia	+	-	+	-	0.2	0.3	0.2	-	-	-	-	-	4.0	0.8	+	-	0.5	-	-	-	-
Olearia erubescens	+	+	-	-	+	+	+	-	-	-	-	+	0.1	+	-	-	+	-	-	-	-
Celmisia saxifraga	-	-	0.3	1.0	-	-	-	0.3	+	4.6	-	-	-	-	0.1	+	-	-	-	-	-
Cyathodes dealbata	-	-	1.5	1.5	-	-	-	0.5	1.7	14.8	-	-	-	+	1.4	0.1	-	-	-	-	-
Diselma archeri	-	-	4.7	4.0	-	-	-	0.1	14.9	5.5	-	-	-	0.2	+	8.4	-	-	-	0.3	-
Erigeron stellatus	-	-	3.7	+	-	-	-	1.7	0.2	4.1	-	-	-	-	0.1	0.4	-	-	-	+	-
Microcachrys tetragona	-	-	3.1	6.8	-	-	-	0.3	4.3	20.1	-	-	-	0.2	1.2	1.3	-	-	-	0.3	-
Oreobolus acutifolius	0.3	-	4.1	+	-	0.2	+	0.9	0.8	3.3	-	-	+	-	+	+	-	-	-	-	-

TABLE 10.3 (Continued) An ordered two-way table of the mean percentage cover of species in each of 21 noda.

	NODUM																				
	14	3	19	17	6	15	5	12	16	11	20	18	13	2	10	9	7	1	4	8	21
NUMBER OF QUADRATS	21	31	20	15	24	24	14	24	21	12	6	18	18	35	22	18	13	12	24	19	7
MEAN ALTITUDE (m)	1026	1090	1198	1263	985	1038	1062	1235	1245	1293	1007	1076	1046	1142	1238	1318	1040	1095	1174	1259	1368
MEAN DRAINAGE SCORE	1.3	1.3	2.6	1.1	2.9	2.9	2.9	3.2	3.0	3.0	4.2	4.0	4.1	4.1	4.0	3.9	5.0	4.9	4.9	4.7	5.0
Acaena novae-zelandiae	-	-	-	-	0.2	-	-	-	-	-	+	+	-	-	-	-	0.1	-	+	-	-
Aristotelia peduncularis	-	-	-	-	0.2	-	-	-	-	-	+	0.1	-	+	-	-	0.6	+	+	-	-
Atherosperma moschatum	-	-	-	-	-	-	-	-	-	-	0.2	0.1	-	-	-	-	0.5	+	+	+	-
Athrotaxis selaginoides	-	-	-	-	+	-	-	-	+	-	3.3	-	-	-	-	0.3	0.4	0.5	-	-	-
Blechnum wattsii	-	-	-	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
Cyathodes glauca	-	-	-	-	0.3	0.2	-	-	-	-	0.1	0.7	0.5	-	-	-	1.3	+	-	-	-
Eucryphia milliganii	-	-	-	-	3.5	-	-	-	-	-	14.4	-	-	-	-	-	-	-	-	-	-
Olearia persoonioides	+	-	-	-	0.1	-	-	-	-	-	0.1	+	+	+	-	-	-	-	+	-	-
Phyllocladus aspleniifolius	-	-	-	-	-	-	-	-	-	-	0.1	+	-	+	-	-	0.4	+	+	-	-
Pittosporum bicolor	-	-	-	-	+	-	-	+	-	-	0.1	+	+	-	-	-	0.2	+	-	-	-
Viola hederacea	-	+	-	-	-	-	-	-	-	-	+	+	+	+	-	-	+	+	-	-	-
Cardamine heterophylla	-	-	-	-	-	-	-	-	-	-	+	+	+	+	-	-	0.2	0.1	0.1	-	-
Geranium potentilloides	-	-	-	-	+	+	-	-	-	+	+	+	+	+	+	-	0.2	0.1	+	-	-
Nothofagus cunninghamii	-	-	+	-	1.2	0.7	+	0.2	-	-	25.2	16.3	-	-	-	-	-	21.4	0.2	-	-
Oxalis lactea	-	-	-	-	+	+	-	-	-	+	0.1	0.1	-	-	+	-	+	0.2	+	-	-
Polystichum proliferum	-	-	-	-	-	-	-	-	-	-	+	0.1	-	-	-	-	0.6	0.2	0.1	+	-
Richea pandanifolia	-	-	+	-	+	+	+	0.5	1.1	-	11.0	0.9	-	-	-	0.3	0.6	2.8	0.2	+	-
Senecio leptocarpus	-	-	-	-	-	+	+	+	+	-	0.4	+	+	-	+	-	-	0.3	+	-	-
Cyathodes straminea	-	+	-	-	0.3	0.3	+	0.3	+	+	6.2	4.0	0.9	1.9	2.1	0.7	2.2	12.8	5.9	3.0	-
Deyeuxia monticola	-	-	-	-	+	+	-	+	-	+	0.1	0.2	0.1	0.1	0.2	+	1.3	0.3	0.7	+	-
Lagenophora stipitata	-	-	-	-	+	+	+	+	-	-	+	0.1	+	0.1	0.1	-	0.1	0.1	0.1	+	+
Olearia phlogopappa	-	-	-	-	-	+	-	-	-	-	-	0.1	0.1	0.2	0.3	-	1.2	0.6	0.3	+	-
Olearia pinifolia	-	-	-	-	+	+	-	0.1	+	-	0.1	1.6	+	0.6	0.6	-	3.2	4.3	5.7	0.4	-
Trochocarpa cunninghamii	-	-	+	-	2.1	+	-	0.5	1.1	-	11.9	3.1	-	0.5	0.3	2.1	1.8	12.0	4.8	2.7	-
Trochocarpa thymifolia	-	-	+	-	0.3	0.1	+	0.2	-	-	-	4.3	4.2	2.5	0.6	-	4.0	2.8	4.1	-	-
Archeria serpyllifolia	-	-	-	-	-	-	-	0.3	0.1	2.6	-	-	-	-	+	15.2	-	-	-	1.8	8.9
Cheesemannia radicata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	0.2
Epilobium gunnianum	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	+	0.1
Gaultheria depressa	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	0.2	-	-	-	+	+
Ourisia integrifolia	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	0.1	-	-	-	-	+
Cyathodes parvifolia	+	-	+	-	6.4	1.5	+	+	-	-	1.3	4.6	6.6	1.2	+	-	13.4	2.9	0.9	+	-
Eucalyptus coccifera	1.2	+	0.3	-	12.2	13.6	5.9	0.5	-	-	-	23.7	32.3	24.5	0.5	-	36.9	27.7	33.0	0.3	-
Gaultheria hispida	-	-	-	-	0.3	+	-	-	+	-	2.0	0.8	0.1	+	-	-	1.0	2.0	0.3	-	-
Orites diversifolia	-	-	0.6	-	4.6	2.1	-	0.5	0.3	-	8.7	5.4	0.4	+	-	-	4.6	1.0	0.5	-	-
Telopea truncata	-	-	0.3	-	3.6	2.3	0.5	0.2	-	-	2.9	2.9	2.8	0.8	0.1	-	1.3	1.5	0.5	-	-
Cyathodes petiolaris	-	-	0.1	-	-	-	-	1.2	0.3	0.1	-	-	-	0.7	8.0	0.1	-	-	0.2	3.2	-
Danthonia fortuna-hibernae	+	-	+	+	-	-	-	0.1	+	0.2	-	+	-	+	0.1	0.1	+	+	+	+	+
Helichrysum backhousii	-	+	0.5	0.5	-	-	+	4.6	1.6	7.9	1.1	0.3	-	0.7	4.1	24.9	-	3.5	1.7	5.1	0.8
Olearia ledifolia	-	+	0.1	0.1	+	+	+	1.2	0.1	0.6	1.0	0.1	+	1.3	2.6	0.6	1.0	1.1	1.6	2.3	+
Podocarpus lawrencii	-	-	+	-	-	-	-	0.6	3.2	0.6	-	0.3	-	1.3	6.8	4.6	+	0.1	8.6	10.1	4.4

TABLE 10.3 (Continued) An ordered two-way table of the mean percentage cover of species in each of 21 noda.

	NODUM																					
	14	3	19	17	6	15	5	12	16	11	20	18	13	2	10	9	7	1	4	8	21
NUMBER OF QUADRATS	21	31	20	15	24	24	14	24	21	12	6	18	18	35	22	18	13	12	24	19	7
MEAN ALTITUDE (m)	1026	1090	1198	1263	985	1038	1062	1235	1245	1293	1007	1076	1046	1142	1238	1318	1040	1095	1174	1259	1368
MEAN DRAINAGE SCORE	1.3	1.3	2.6	1.1	2.9	2.9	2.9	3.2	3.0	3.0	4.2	4.0	4.1	4.1	4.0	3.9	5.0	4.9	4.9	4.7	5.0
Agrostis parviflora	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	+	0.4	+	+	-	-
Blechnum penna-marina	-	-	-	-	+	-	-	-	-	+	-	+	-	-	+	+	-	0.1	-	-	+
Epilobium sarmentaceum	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	+	+	-
Grammitis armstrongii	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	0.1	-	0.1	-	0.1
Helichrysum ledifolium	-	0.2	-	-	-	-	0.8	-	-	-	-	+	-	1.4	0.5	-	-	-	+	-	-
Lissanthe montana	-	-	-	-	-	-	-	+	-	-	-	-	+	0.2	0.1	+	+	+	0.1	0.1	0.1
Luzula australasica	-	-	-	+	-	-	-	+	-	-	+	+	+	+	+	-	+	+	+	+	-
Plantago tasmanica	+	+	-	-	+	+	+	+	-	+	-	+	-	+	0.1	-	+	+	-	-	-
Acaena montana	-	+	-	0.1	-	-	-	0.1	+	0.5	-	-	-	-	+	+	0.1	+	-	+	-
Craspedia alpina	+	+	+	+	-	+	-	+	+	0.1	-	-	-	-	+	+	-	-	-	-	-
Euphrasia gibbsiae	-	+	0.1	0.1	-	-	-	0.3	+	0.1	-	-	-	+	0.1	+	-	+	-	+	+
Ewartia planchonii	-	-	+	+	-	-	-	+	+	+	-	-	+	-	+	+	-	-	+	+	+
Astelia alpina	3.5	22.1	5.4	13.4	4.9	3.5	7.5	11.4	20.7	9.9	0.1	3.3	0.7	6.0	4.2	17.5	+	2.4	2.3	3.7	2.0
Athrotaxis cupressoides	-	-	1.3	-	+	-	+	0.2	2.6	-	1.8	-	-	-	-	+	-	-	-	0.3	-
Bellendena montana	0.1	0.6	0.4	0.2	-	-	0.1	0.4	0.2	0.7	+	-	-	0.1	0.1	0.3	-	-	+	0.3	+
Celmisia longifolia	+	+	0.1	0.1	+	+	0.1	0.2	+	0.1	+	+	0.1	0.2	0.2	+	-	-	0.1	0.1	-
Epacris serpyllifolia	8.0	21.1	16.4	9.4	0.8	17.2	23.4	17.7	5.8	9.6	0.9	1.4	8.2	8.3	8.5	+	+	-	0.7	4.8	0.1
Leptospermum rupestre	-	0.4	1.9	+	+	0.2	1.9	4.7	1.3	0.5	-	2.8	-	5.3	5.0	+	+	+	0.9	3.0	-
Lycopodium australianum	-	+	-	+	-	-	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-
Lycopodium fastigiatum	+	+	+	0.1	+	+	0.1	0.1	0.3	0.3	0.2	+	+	0.2	0.1	0.1	-	0.1	+	+	-
Lycopodium scariosum	0.1	-	0.2	+	-	+	-	0.1	+	+	-	-	+	+	0.1	+	-	-	-	0.1	-
Mitrasacme montana	+	+	+	+	+	+	+	+	+	0.5	-	-	+	+	+	+	-	-	-	-	-
Orites acicularis	1.8	3.7	2.0	1.7	-	1.8	15.6	6.3	5.0	3.8	1.0	-	0.3	2.9	2.8	7.8	-	+	+	4.4	-
Pentachondra pumila	-	0.2	2.0	0.9	-	+	+	3.7	1.8	4.7	-	-	3.3	1.8	3.1	0.7	-	-	+	+	-
Pimelea sericea	-	0.2	+	0.1	+	0.2	+	0.3	1.4	+	-	-	0.6	1.0	1.8	0.3	-	-	0.3	+	-
Poa gunnii	1.0	3.3	1.9	1.4	+	1.6	3.7	3.2	1.3	8.6	+	+	0.1	1.5	3.4	+	+	0.5	+	0.1	+
Richea scoparia	+	0.2	2.6	9.0	10.2	1.6	2.2	9.7	4.9	1.0	18.4	3.5	0.3	3.0	1.0	1.7	-	0.9	1.6	4.0	1.7
Uncinia compacta	+	0.1	0.1	0.6	+	0.3	0.2	0.2	0.8	0.1	-	0.2	0.1	0.4	0.1	0.2	0.1	0.1	0.2	0.1	+
Coprosma nitida	+	+	+	+	1.6	0.2	0.1	0.5	0.5	0.2	2.9	3.5	2.4	2.3	2.0	0.6	10.4	4.7	5.6	2.9	1.9
Drimys lanceolata	-	0.1	0.4	+	0.4	0.2	0.2	1.6	1.8	0.1	3.8	4.4	1.8	5.2	3.4	2.6	7.7	8.7	9.1	3.6	1.1
Exocarpos humifusus	+	+	0.1	+	0.1	0.1	0.1	1.0	0.1	-	0.1	1.0	4.9	2.6	5.2	+	0.4	1.1	2.9	1.3	-
Gonocarpus serpyllifolius	+	+	+	+	+	0.1	0.1	0.1	0.1	0.1	+	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.4	+	-
Hierochloe redolens	+	+	+	+	-	+	+	0.1	0.1	0.1	+	+	-	+	0.1	0.1	0.2	0.2	0.2	0.2	0.1
Orites revoluta	0.9	1.2	2.8	0.1	0.6	2.5	4.4	5.5	1.1	1.7	3.7	2.7	9.1	8.7	15.0	2.9	-	1.9	4.7	3.6	1.6
Richea sprengelioides	+	0.2	0.5	0.1	1.3	1.5	2.6	6.3	2.6	3.8	4.4	1.2	12.1	16.7	17.5	5.7	+	3.6	7.6	6.5	0.9
Rubus gunnianus	+	0.1	+	+	0.1	0.1	0.1	0.1	0.1	-	-	0.2	0.1	0.2	0.2	+	0.1	0.3	0.4	0.1	-

TABLE 10.3 (Continued) An ordered two-way table of the mean percentage cover of species in each of 21 noda.

	NODUM																					
	14	3	19	17	6	15	5	12	16	11	20	18	13	2	10	9	7	1	4	8	21
NUMBER OF QUADRATS	21	31	20	15	24	24	14	24	21	12	6	18	18	35	22	18	13	12	24	19	7
MEAN ALTITUDE (m)	1026	1090	1198	1263	985	1038	1062	1235	1245	1293	1007	1076	1046	1142	1238	1318	1040	1095	1174	1259	1368
MEAN DRAINAGE SCORE	1.3	1.3	2.6	1.1	2.9	2.9	2.9	3.2	3.0	3.0	4.2	4.0	4.1	4.1	4.0	3.9	5.0	4.9	4.9	4.7	5.0
Gymnoshoenus sphaerocephalus	19	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melaleuca squamea	29	3	-	-	25	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Restio complanatus	62	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Boronia citriodora	90	77	-	-	13	67	86	-	-	-	-	6	39	11	-	-	-	-	-	-	-
Brachycome tenuiscapa	5	10	-	-	-	13	43	-	-	-	-	-	11	3	9	-	-	-	-	-	-
Campynema lineare	14	3	20	-	8	29	7	-	-	-	17	-	-	-	-	-	-	-	-	-	-
Diplarrena latifolia	95	97	5	-	13	67	93	-	-	-	-	-	39	14	-	-	-	-	-	-	-
Gleichenia alpina	100	100	10	-	17	38	93	-	-	-	-	-	6	11	-	-	-	-	-	-	-
Hakea epiglottis	43	13	-	-	8	71	36	-	-	-	-	-	11	-	-	-	-	-	-	-	-
Helichrysum hookeri	24	97	-	-	-	-	36	-	-	-	-	-	-	3	-	-	-	-	-	-	-
Lepidosperma filiforme	100	77	-	-	13	38	36	-	-	-	-	-	22	-	-	-	-	-	-	-	-
Oreobolus oxycarpus	67	19	-	-	21	54	50	4	-	-	-	-	6	-	5	-	-	-	-	-	-
Restio australis	81	48	-	-	-	13	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dracophyllum milliganii	-	-	25	-	-	-	-	4	5	-	-	-	-	-	-	-	-	-	-	-	-
Helichrysum pumilum	-	-	70	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
Persoonia gunnii	-	-	45	-	13	8	-	17	-	-	-	-	22	-	-	-	-	-	-	-	-
Lepidosperma lineare var. inops	5	3	45	-	-	-	7	4	-	8	-	-	-	3	-	-	-	-	-	-	-
Abrotanella forsteroides	5	19	-	93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Abrotanella scapigera	-	-	-	33	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
Carpha sp. nov.	-	-	5	73	-	-	-	-	10	8	-	-	-	-	-	6	-	-	-	-	-
Diplaspis cordifolia	14	16	10	67	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
Dracophyllum minimum	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ewartia meridithae	10	3	10	47	-	-	-	-	10	8	-	-	-	-	-	-	-	-	-	-	-
Mitrasacme archeri	24	19	25	73	-	-	7	-	5	-	-	-	-	-	-	-	-	-	-	-	-
Pterygopappus lawrencii	5	6	-	93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Actinotus suffocata	29	3	35	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex appressa	5	23	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Centrolepis monogyna	33	13	15	20	-	4	7	-	5	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 10.4 An ordered two-way table of the frequencies of occurrence (%) of species in each of 21 noda. The noda were produced by Minimum Sum-of-squares Clustering of the total data set (cover class data), followed by iterative relocation. The species have been arranged in groups, largely according to the 20 group classification produced by flexible clustering (beta=-0.25) of the TWO-STEP dissimilarity matrix, computed from cover class data, normalised by species. The noda have been grouped into four series, according to their mean drainage scores, and ordered by mean altitude within each series. Subsequently, the species groups were ordered so as to emphasise the compositional gradient with altitude within each series of noda.

	NODUM																				
	14	3	19	17	6	15	5	12	16	11	20	18	13	2	10	9	7	1	4	8	21
NUMBER OF QUADRATS	21	31	20	15	24	24	14	24	21	12	6	18	18	35	22	18	13	12	24	19	7
MEAN ALTITUDE (m)	1026	1090	1198	1263	985	1038	1062	1235	1245	1293	1007	1076	1046	1142	1238	1318	1040	1095	1174	1259	1368
MEAN DRAINAGE SCORE	1.3	1.3	2.6	1.1	2.9	2.9	2.9	3.2	3.0	3.0	4.2	4.0	4.1	4.1	4.0	3.9	5.0	4.9	4.9	4.7	5.0
Baeckea gunniana	95	90	60	33	13	42	100	17	14	-	-	-	6	17	-	-	-	-	-	-	-
Empodisma minus	100	100	90	93	96	100	100	54	19	17	-	6	44	46	-	-	8	-	8	-	-
Richea gunnii	5	26	-	7	8	4	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scirpus aucklandicus	10	32	20	20	8	25	50	17	14	25	-	-	17	9	5	6	-	-	-	-	-
Sprengelia incarnata	86	52	75	60	25	8	14	13	5	-	-	-	-	-	5	-	-	-	-	-	-
Senecio pectinatus var. pectinatus	57	13	55	13	-	21	21	17	5	8	-	-	6	26	14	11	-	-	-	-	-
Carpha alpina	100	81	100	100	8	50	64	63	76	83	-	6	-	14	32	6	-	8	-	16	-
Danthonia pauciflora	10	10	60	93	-	-	-	13	38	33	-	-	-	-	-	6	-	-	-	-	-
Drosera arcturi	52	19	75	87	4	4	14	13	14	-	-	-	-	-	-	6	-	-	-	-	-
Erigeron pappochroma	95	68	30	93	4	13	43	58	52	42	-	-	-	9	27	33	-	8	-	16	43
Euphrasia striata	29	16	95	60	13	29	36	50	19	33	50	6	11	11	27	-	-	-	-	-	-
Gentianella diemensis	19	39	20	87	-	13	29	33	33	92	-	-	-	3	14	50	-	-	-	5	14
Microstrobos niphophilus	19	23	100	93	-	-	29	75	90	17	-	-	-	17	9	-	-	-	-	11	-
Oreobolus pumilio	33	45	90	100	-	8	29	42	38	33	-	-	-	-	5	6	-	-	-	-	-
Banksia marginata	-	-	-	-	58	8	-	-	-	-	-	-	22	-	-	-	-	-	-	-	-
Billardiera longiflora	-	-	-	-	8	-	-	-	-	-	-	-	11	-	-	-	8	-	-	-	-
Blandfordia punicea	-	-	10	-	-	-	-	-	-	-	-	-	28	3	-	-	-	-	-	-	-
Leptospermum nitidum	5	-	-	-	17	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-
Pimelea drupacea	-	-	-	-	4	8	7	-	-	-	-	6	-	-	-	-	8	-	-	-	-
Monotoca submutica var. autumnalis	-	-	-	-	4	-	-	-	-	-	-	-	22	-	-	-	-	-	-	-	-
Bauera rubioides	81	26	50	-	100	100	86	8	-	-	-	100	100	91	-	-	46	-	33	-	-
Eucalyptus subcrenulata	-	3	-	-	96	21	29	-	-	-	50	61	61	3	-	-	46	8	-	-	-
Eucalyptus urnigera	-	3	-	-	8	58	7	-	-	-	-	11	17	-	-	-	-	-	-	-	-
Gahnia grandis	-	3	-	-	100	50	14	-	-	-	-	11	28	-	-	-	8	-	4	-	-
Hakea lissosperma	-	-	-	-	63	38	7	-	-	-	-	6	67	-	-	-	-	-	-	-	-
Leptospermum lanigerum	52	19	-	-	100	100	71	-	-	-	17	67	67	14	-	-	23	17	8	-	-
Lomatia polymorpha	14	-	15	-	67	50	21	-	-	-	-	11	61	14	-	-	-	-	-	-	-
Monotoca empetrifolia	5	-	5	-	8	33	43	-	-	-	-	-	100	23	5	-	15	-	-	-	-
Olearia erubescens	5	6	-	-	38	38	21	-	-	-	-	33	83	14	-	-	8	-	-	-	-
Celmisia saxifraga	-	-	5	73	-	-	-	17	5	83	-	-	-	-	9	6	-	-	-	-	-
Cyathodes dealbata	-	-	50	53	-	-	-	25	62	92	-	-	-	6	23	17	-	-	-	-	-
Diselma archeri	-	-	65	73	-	-	-	17	76	42	-	-	-	3	5	39	-	-	-	11	-
Erigeron stellatus	-	-	90	20	-	-	-	63	71	75	-	-	-	-	18	28	-	-	-	11	-
Microcachrys tetragona	-	-	65	67	-	-	-	25	62	83	-	-	-	6	18	28	-	-	-	5	-
Oreobolus acutifolius	29	-	90	20	-	4	14	71	71	83	-	-	6	-	5	11	-	-	-	-	-

TABLE 10.4 (Continued) An ordered two-way table of the frequency of occurrence (%) of species in each of 21 noda.

	NODUM																				
	14	3	19	17	6	15	5	12	16	11	20	18	13	2	10	9	7	1	4	8	21
NUMBER OF QUADRATS	21	31	20	15	24	24	14	24	21	12	6	18	18	35	22	18	13	12	24	19	7
MEAN ALTITUDE (m)	1026	1090	1198	1263	985	1038	1062	1235	1245	1293	1007	1076	1046	1142	1238	1318	1040	1095	1174	1259	1368
MEAN DRAINAGE SCORE	1.3	1.3	2.6	1.1	2.9	2.9	2.9	3.2	3.0	3.0	4.2	4.0	4.1	4.1	4.0	3.9	5.0	4.9	4.9	4.7	5.0
Acaena novae-zelandiae	-	-	-	-	4	-	-	-	-	-	17	11	-	-	-	-	54	-	4	-	-
Aristotelia peduncularis	-	-	-	-	33	-	-	-	-	-	17	33	-	3	-	-	54	8	8	-	-
Atherosperma moschatum	-	-	-	-	-	-	-	-	-	-	50	11	-	-	-	-	31	8	4	5	-
Athrotaxis selaginoides	-	-	-	-	4	-	-	-	5	-	33	-	-	-	-	6	8	8	-	-	-
Blechnum wattsii	-	-	-	-	4	-	-	-	-	-	33	11	-	-	-	-	-	-	-	-	-
Cyathodes glauca	-	-	-	-	17	4	-	-	-	-	17	39	44	-	-	-	31	8	-	-	-
Eucryphia milliganii	-	-	-	-	29	-	-	-	-	-	83	-	-	-	-	-	-	-	-	-	-
Olearia persoonioides	5	-	-	-	29	-	-	-	-	-	33	6	6	3	-	-	-	-	4	-	-
Phyllocladus asplenifolius	-	-	-	-	-	-	-	-	-	-	17	11	-	3	-	-	8	17	4	-	-
Pittosporum bicolor	-	-	-	-	13	-	-	4	-	-	17	6	6	-	-	-	54	8	-	-	-
Viola hederacea	-	3	-	-	-	-	-	-	-	-	17	33	11	3	-	-	15	25	-	-	-
Cardamine heterophylla	-	-	-	-	-	-	-	-	-	-	17	22	6	9	-	-	77	67	42	-	-
Geranium potentilloides	-	-	-	-	4	13	-	-	-	8	17	39	28	11	5	-	100	67	25	-	-
Nothofagus cunninghamii	-	-	5	-	29	13	7	4	-	-	100	78	-	-	-	-	-	92	4	-	-
Oxalis lactea	-	-	-	-	8	8	-	-	-	8	67	50	-	-	9	-	8	83	4	-	-
Polystichum proliferum	-	-	-	-	-	-	-	-	-	-	17	28	-	-	-	-	62	67	25	5	-
Richea pandanifolia	-	-	5	-	4	13	7	25	33	-	83	17	-	-	-	6	31	50	4	5	-
Senecio leptocarpus	-	-	-	-	-	4	7	4	5	-	83	39	6	-	14	-	-	58	8	-	-
Cyathodes straminea	-	3	-	-	17	21	14	17	14	8	100	83	17	89	55	28	69	100	96	68	-
Deyeuxia monticola	-	-	-	-	8	13	-	4	-	8	67	67	61	43	64	6	100	83	79	16	-
Lagenophora stipitata	-	-	-	-	13	8	7	4	-	-	17	67	28	37	32	-	62	75	50	21	14
Olearia phlogopappa	-	-	-	-	-	8	-	-	-	-	-	50	39	31	14	-	92	50	79	5	-
Olearia pinifolia	-	-	-	-	4	13	-	13	10	-	33	61	6	43	23	-	92	100	100	37	-
Trochocarpa cunninghamii	-	-	5	-	50	4	-	13	38	-	100	61	-	17	23	39	54	100	63	63	-
Trochocarpa thymifolia	-	-	5	-	17	21	7	8	-	-	-	83	67	43	27	-	46	67	54	-	-
Archeria serpyllifolia	-	-	-	-	-	-	-	8	24	33	-	-	-	-	5	94	-	-	-	37	100
Cheesemannia radicata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	57
Epilobium gunnianum	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	17	-	-	-	5	71
Gaultheria depressa	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	39	-	-	-	5	14
Ourisia integrifolia	-	-	-	13	-	-	-	-	5	-	-	-	-	-	-	17	-	-	-	-	43
Cyathodes parvifolia	5	-	5	-	96	71	21	4	-	-	83	94	100	51	5	-	100	100	50	5	-
Eucalyptus coccifera	10	3	15	-	58	88	64	8	-	-	-	94	100	97	9	-	92	100	83	5	-
Gaultheria hispida	-	-	-	-	46	4	-	-	5	-	67	78	22	9	-	-	62	58	21	-	-
Orites diversifolia	-	-	10	-	58	42	-	8	5	-	100	89	22	6	-	-	77	25	8	-	-
Telopea truncata	-	-	20	-	96	58	29	4	-	-	83	89	78	20	9	-	38	50	13	-	-
Cyathodes petiolaris	-	-	15	-	-	-	-	29	10	17	-	-	-	20	68	11	-	-	4	63	-
Danthonia fortuna-hibernae	5	-	40	7	-	-	-	54	38	67	-	6	-	11	68	78	8	8	29	42	29
Helichrysum backhousii	-	3	65	73	-	-	7	92	71	100	50	11	-	37	100	100	-	50	54	95	14
Olearia ledifolia	-	10	70	53	4	4	14	83	57	50	33	22	17	69	100	61	46	50	71	95	29
Podocarpus lawrencii	-	-	10	-	-	-	-	38	71	33	-	6	-	43	68	50	8	17	79	89	43

TABLE 10.4 (Continued) An ordered two-way table of the frequency of occurrence (%) of species in each of 21 noda.

	NODUM																				
	14	3	19	17	6	15	5	12	16	11	20	18	13	2	10	9	7	1	4	8	21
NUMBER OF QUADRATS	21	31	20	15	24	24	14	24	21	12	6	18	18	35	22	18	13	12	24	19	7
MEAN ALTITUDE (m)	1026	1090	1198	1263	985	1038	1062	1235	1245	1293	1007	1076	1046	1142	1238	1318	1040	1095	1174	1259	1368
MEAN DRAINAGE SCORE	1.3	1.3	2.6	1.1	2.9	2.9	2.9	3.2	3.0	3.0	4.2	4.0	4.1	4.1	4.0	3.9	5.0	4.9	4.9	4.7	5.0
Agrostis parviflora	-	-	-	-	-	-	-	-	-	-	-	6	-	9	5	6	8	8	8	-	-
Blechnum penna-marina	-	-	-	-	4	-	-	-	-	8	-	11	-	-	23	22	-	25	-	-	14
Epilobium sarmentaceum	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	8	13	5	-
Grammitis armstrongii	-	-	-	-	-	-	-	-	-	-	-	-	11	14	-	11	46	-	33	-	14
Helichrysum ledifolium	-	10	-	-	-	-	14	-	-	-	-	6	-	26	9	-	-	-	4	-	-
Lissanthe montana	-	-	-	-	-	-	-	4	-	-	-	-	6	9	32	6	8	8	21	11	14
Luzula australasica	-	-	-	13	-	-	-	4	-	-	17	6	11	6	32	-	8	25	4	5	-
Plantago tasmanica	5	13	-	-	4	13	29	8	-	8	-	22	-	6	18	-	8	25	-	-	-
Acaena montana	-	13	-	33	-	-	-	25	29	17	-	-	-	-	5	11	23	8	-	5	-
Craspedia alpina	10	29	5	40	-	4	-	17	19	17	-	-	-	-	5	6	-	-	-	-	-
Euphrasia gibbsiae	-	10	10	53	-	-	-	21	19	33	-	-	-	6	14	17	-	8	-	5	14
Ewartia planchonii	-	-	5	20	-	-	-	21	14	8	-	-	6	-	14	11	-	-	4	5	14
Astelia alpina	95	97	95	100	50	83	93	96	100	92	67	72	39	97	86	100	23	92	50	74	100
Athrotaxis cupressoides	-	-	10	-	4	-	7	8	14	-	33	-	-	-	-	6	-	-	-	5	-
Bellendena montana	24	39	55	47	-	-	29	50	57	92	33	-	-	23	36	72	-	-	4	16	14
Celmisia longifolia	76	71	95	67	4	46	71	75	33	58	33	17	56	66	86	6	-	-	33	21	-
Epacris serpyllifolia	100	100	100	100	38	96	100	100	86	42	17	17	72	89	77	6	8	-	21	79	14
Leptospermum rupestre	-	6	80	7	4	4	21	67	71	17	-	6	-	63	64	6	8	8	21	26	-
Lycopodium australianum	-	3	-	20	-	-	7	8	29	17	33	6	6	11	9	17	15	-	4	5	-
Lycopodium fastigiatum	5	10	10	47	8	13	50	38	33	83	50	28	17	23	50	22	-	17	8	16	-
Lycopodium scariosum	10	-	50	27	-	4	-	50	19	17	-	-	6	6	45	11	-	-	-	16	-
Mitrasacme montana	10	16	40	13	4	4	21	38	10	33	-	-	6	9	23	11	-	-	-	-	-
Orites acicularis	33	65	90	80	-	25	93	96	95	83	33	-	6	49	68	94	-	8	8	95	-
Pentachondra pumila	-	13	95	73	-	13	14	92	86	100	-	-	56	29	77	44	-	-	8	11	-
Pimelea sericea	-	16	10	20	4	25	21	21	38	8	-	-	17	23	41	6	-	-	8	5	-
Poa gunnii	71	94	95	93	25	92	100	92	86	92	17	33	39	80	100	28	8	50	17	32	14
Richea scoparia	5	16	75	100	75	38	36	92	95	25	83	44	6	40	27	22	-	17	25	74	43
Uncinia compacta	24	87	70	87	25	83	93	88	100	67	-	72	44	83	77	83	62	67	54	63	29
Coprosma nitida	5	6	5	20	67	75	36	50	76	50	100	100	94	91	95	78	100	100	100	95	100
Drimys lanceolata	-	26	70	13	67	54	50	79	86	33	100	100	83	100	95	83	100	100	100	100	71
Exocarpos humifusus	5	6	35	7	17	25	29	42	29	-	17	33	100	63	95	6	15	50	83	58	-
Gonocarpus serpyllifolius	14	42	10	7	29	58	64	54	57	17	33	67	67	80	82	28	62	58	42	16	-
Hierochloe redolens	5	29	20	33	-	8	14	58	71	58	17	61	-	43	86	67	92	83	88	84	71
Orites revoluta	43	45	100	33	38	42	93	96	86	83	83	39	83	100	100	83	-	50	75	89	43
Richea sprengelioides	5	16	75	33	29	50	36	100	90	92	67	28	78	100	100	94	8	58	79	100	43
Rubus gunnianus	14	58	10	20	71	75	93	63	52	-	-	78	67	71	73	44	31	92	75	42	-

TABLE 10.4 (Continued) An ordered two-way table of the frequency of occurrence (%) of species in each of 21 noda.

character species for the nodum. Often, they are relatively widespread, and consequently not diagnostic of a narrow range of habitat conditions. In some cases it has been possible to identify "characteristic species" for each nodum. These are species which attain their highest frequency of occurrence in the nodum, although their constancy in the nodum may not be high. Since the noda are arbitrary reference points in a compositional continuum, the differences between adjacent noda are often due to changes in the frequency of occurrence and/or mean cover of species, rather than clear-cut floristic transitions.

The order of description of the noda accords with their arrangement in Tables 10.3 and 10.4. Noda 14, 3 and 17 constitute an altitudinal sequence on poorly drained to waterlogged sites. Nodum 19 is altitudinally intermediate between 3 and 17, but represents somewhat better drainage conditions. Noda 6, 15, 5, 12, 16 and 11 essentially represent an altitudinal sequence on moderately drained sites. However, the differences between 12 and 16 are possibly due to firing history, and nodum 5 is more poorly drained than 15. The series represented by noda 20, 18, 13, 2, 10 and 9 is primarily one of increasing altitude on well drained sites, although the variation between 20, 18 and 13 (which do not differ significantly in mean altitude) has been tentatively related to firing history. Finally, noda 7, 1, 4, 8 and 21 depict a gradient of increasing altitude on boulderfields and screes. Structural nomenclature is based on the system outlined in Table 7.2.

10.3.3.1 Nodum 14 : Lepidosperma filiforme - Gleichenia alpina - Empodisma minus

Nodum 14 typifies the vegetation of poorly drained to waterlogged sites at altitudes between 950 and 1050m. The soils are generally High Moor Peats (Dimmock 1961; see section 6.4). An impermeable iron pan produces a perched water table, which may be almost constantly at or near the surface of the peat.

The structural form of the community is usually open-heath, with the shrub canopy ranging from 0.3 to 0.8m in height. Occasionally, the cover of shrubs may be so low that the community may be better described as closed-sedgeland or closed-sedgeland/fernland. The mean alpha diversity of graminoids reaches its maximum value of 9.5 in this nodum (cf. Figure 8.4).

The constant dominants are the tussock-forming sedge Lepidosperma filiforme, the rhizomatous fern Gleichenia alpina and the cord-rush Empodisma minus. Of these, L. filiforme may be regarded as a characteristic species of the nodum, while G. alpina is a joint characteristic species of noda 14, 3 and 5. The shrubs Baeckea gunniana and Epacris serpyllifolia are constant, but not characteristic, since they are also frequent in several other noda. The characteristic shrubs are Boronia citriodora and Sprengelia incarnata. Other characteristic species include the graminoids Oreobolus oxycarpus, Restio australis and R. complanatus. The graminoids Astelia alpina, Carpha alpina and Diplarrena latifolia, and the herb Erigeron pappochroma are constant, but not faithful.

Largely confined to this nodum and nodum 6, are the shrub

Melaleuca squamea and the hummock sedge Gymnoshoenus sphaerocephalus ("button grass"). These are essentially lowland species which reach their upper altitudinal limit at about 1000m in the study area. Closed-hummock sedgelands and sedgeland/heaths, dominated by button grass, occupy the poorly drained flats on the floor of the Broad River valley, north of Lake Seal (Figure 6.1).

10.3.3.2 Nodum 3 : Gleichenia alpina - Astelia alpina - Epacris serpyllifolia

Nodum 3 may be regarded as the higher altitude equivalent of nodum 14. It typifies the vegetation of poorly drained to waterlogged sites at altitudes between 1050 and 1150m. Structurally, the communities represented are generally open-heaths or closed-heaths, with the height of the shrub stratum ranging from 0.5 to 1m. As in nodum 14, the cover of shrubs may sometimes be less than 10%, in which case the structural form is closed-fernland or closed-fernland/lilyland.

The "constant dominants" are the shrub Epacris serpyllifolia, the lily Astelia alpina and the fern Gleichenia alpina. The shrub Helichrysum hookeri is a good characteristic species, being both constant and faithful to this nodum. Other constant, but not faithful, species include the shrub Baeckea gunniana and the graminoids Carpha alpina, Diplarrena latifolia, Empodisma minus and Poa gunnii, The herbs Celmisia longifolia and Erigeron pappochroma and the graminoids Lepidosperma filiforme, Oreobolus pumilio and Restio australis have frequencies from 40 to 80%, but none is confined to this nodum.

Occasionally, the cover of Helichrysum hookeri is very low and the shrub stratum is dominated by Orites acicularis and the conifer

Microstrobos niphophilus. This may reflect historical patterns of firing, since both the latter species are regarded as fire sensitive (Kirkpatrick, Dickinson and Cantle 1982). In some places, the *Helichrysum hookeri* and *Orites acicularis* - *Microstrobos niphophilus* heaths abut along sharp boundaries, which may reflect fire-lines. In such situations, no change in edaphic conditions is evident at the boundary, and the composition of the ground stratum is identical on both sides. Another observation consistent with the firing history hypothesis, is the frequent dominance of *Microstrobos niphophilus* and *Orites acicularis* along creek margins, where a degree of fire protection is likely.

In situations where the water table is almost constantly at, or near, the surface of the peat, the shrub stratum is generally reduced in cover and diversity, and a characteristic set of species occurs, including the cushion-forming shrub *Abrotanella forsteroides*, the cushion-forming herb *Pterygopappus lawrencii*, the perennial herbs *Diplaspis cordifolia* and *Mitrasacme archeri* and the geophyte *Drosera arcturi*. These species are more typical of the higher altitude nodum 17. Their presence in the wetter phases of nodum 3 suggests that their greater frequency and cover at higher altitudes may be partly connected with the higher precipitation on the more elevated, western plateau surfaces (see section 6.5.3).

10.3.3.3 Nodum 19 : Microstrobos niphophilus - Epacris serpyllifolia

Nodum 19 typifies the vegetation of poorly drained to moderately drained sites in the altitude range 1150-1250m. Within the study area, the majority of sites representing this environmental combination are in the Tarn Shelf region (Figure 6.1). Protection from the prevailing west to south-westerly winds, afforded by the Rodway Range, probably results in a climatic regime less severe than is "normal" for these altitudes elsewhere in the study area. This is reflected in the occurrence on Tarn Shelf of subalpine species, such as Bauera rubioides, Lomatia polymorpha, Telopea truncata and scattered individuals of mallee-form Eucalyptus coccifera, above their usual altitude limits. Most of the Tarn Shelf quadrats included in this nodum are also edaphically distinctive. Scouring by glacial ice has produced smooth bedrock surfaces, over which shallow peats (often c.5cm deep) have developed since deglaciation. Although the vegetational composition of the quadrats in nodum 19 places them in the expected position within the altitude X drainage continuum (Figure 10.2), the unusual exposure and edaphic conditions result in some floristic peculiarities. The shrubs Dracophyllum milliganii and Persoonia gunnii, the herb Helichrysum pumilum and the sedge Lepidosperma lineare var. inops are largely confined to this nodum, though not of high constancy.

The structural form is generally open-heath, with the height of the shrub canopy varying from 0.5 to 1m. The mean number of vascular species per $100m^2$ sample reaches its maximum value of 33 in this nodum.

The major components of the shrub stratum are the constant dominants Microstrobos niphophilus and Epacris serpyllifolia. Other

shrubs of high constancy are Leptospermum rupestre, Orites acicularis, O. revoluta and the prostrate Pentachondra pumila. Constant members of the ground layer are the graminoids Astelia alpina, Carpha alpina, Empodisma minus, Oreobolus acutifolius, O. pumilio and Poa gunnii and the herbs Celmisia longifolia, Erigeron stellatus and Euphrasia striata. Shrubs of intermediate frequency (50-80%) include Richea scoparia, R. spengelioides, the conifer Diselma archeri, and the prostrate conifer Microcachrys tetragona.

10.3.3.4 Nodum 17 : Microstrobos niphophilus - Astelia alpina - Empodisma minus

Nodum 17 typifies the vegetation of poorly drained to waterlogged sites at altitudes from 1250 to 1300m. Within the study area, this combination of drainage and altitude is largely confined to Mawson Plateau (Figure 6.1). Such sites are level or gently sloping, and the development of permanent drainage channels is prevented by the damming activities of cushion-forming shrubs and sedges. Numerous shallow tarns occur behind the cushion-plant dams.

The communities are usually open-heaths, with the shrub stratum ranging from 0.3 to 0.5m in height. The relatively low stature of the shrubs reflects the extreme exposure to prevailing winds on Mawson Plateau. Most shrubs are noticably wind-pruned. Sometimes the cover of erect shrubs is very low, and the community is dominated by cushion-forming shrubs. The structural form may then be described as cushion closed-heath or cushion open-heath (Table 7.2). The mean alpha diversity of vascular species is 32 per $100m^2$ sample, only marginally less than nodum 19. In this nodum, perennial herbs attain their maximum

diversity of 8.9 species per $100m^2$ (cf. Figure 8.4).

The constant dominants are the coniferous shrub Microstrobos niphophilus and the graminoids Astelia alpina and Empodisma minus, none of which is faithful to this nodum. Other constant, but not faithful, species are the shrubs Epacris serpyllifolia and Richea scoparia, the graminoids Carpha alpina and Poa gunnii and the herbs Erigeron pappochroma, Drosera arcturi and Gentianella diemensis. Characteristic species are the cushion-forming shrubs Abrotanella forsteroides and Dracophyllum minimum, the cushion-forming herbs Ewartia meridithae and Pterygopappus lawrencii, the mat-forming sedges Carpha sp. nov. and Oreobolus pumilio, the herbs Abrotanella scapigera, Diplaspis cordifolia and Mitrasacme archeri and the grass Danthonia pauciflora. The cushion-plants and mat-forming sedges sometimes coalesce, forming a compact, gently undulating surface, in which other species may be epiphytic. Both Empodisma minus and Sprengelia incarnata are represented in this nodum by diminutive forms which may, upon further study, be found to be genetically distinct from their subalpine counterparts.

10.3.3.5 Nodum 6 : Eucalyptus subcrenulata - Leptospermum lanigerum - Bauera rubioides

Nodum 6 represents the vegetation of moderately drained sites at altitudes between 900 and 1000m. The soils are generally developed over glacial or periglacial deposits (section 6.4), and may have a shallow surface layer of peat or peaty clay-loam. The structural form is usually open-forest, with the height of the tree stratum varying from 10 to 25m. There is a dense layer of subordinate trees and tall shrubs up to 5m in height and an equally dense stratum of low shrubs and

graminoids. The multi-layered structure accounts for the fact that mean total cover attains a maximum of 209% in this nodum (cf. Figure 8.2). Herbs are uncommon, probably due to the relatively low light intensity on the forest floor.

The constant dominants are the tree Eucalyptus subcrenulata ("yellow gum"), the subordinate tree Leptospermum lanigerum ("woolly tea-tree") and the low, scrambling shrub Bauera rubioides. Of these, only E. subcrenulata attains its highest frequency of occurrence in this nodum. Eucalyptus coccifera ("snow gum") is co-dominant with E. subcrenulata in about 60% of stands, generally being somewhat taller, but of lower cover.

Characteristic species, which are confined to nodum 6, or reach their highest frequency there, are the subordinate trees Banksia marginata and Leptospermum nitidum, the shrub Telopea truncata and the large, tussock-forming sedge Gahnia grandis. The subordinate tree Hakea lissosperma is virtually confined to this nodum and nodum 13. Species which are constant, but not faithful, include the shrub Cyathodes parvifolia and the twining cord-rush Empodisma minus. The shrub Richea scoparia occurs in about 75% of quadrats. Occurrences of the shrub Tetracarpaea tasmanica were confined to this nodum, although this species was excluded from the numerical analyses due to its infrequency in the data set.

10.3.3.6 Nodum 15 : Leptospermum lanigerum - Bauera rubioides - Epacris serpyllifolia

Nodum 15 typifies the vegetation of moderately drained sites from 1000 to 1150m in altitude. Soils are similar to those of nodum 6. The structural form is usually woodland, although the cover of eucalypts is sometimes so low that the community may be regarded as dwarf closed-forest or dwarf open-forest, depending on the cover of Leptospermum lanigerum. The dominant tree stratum varies from 10 to 20m in height, with the subordinate tree layer generally being less than 5m high. There is also a dense layer of low shrubs and a fairly well developed ground layer of graminoids and herbs. Mean total cover is 192%, not much lower than nodum 6.

The constant dominants are Leptospermum lanigerum, Epacris serpyllifolia and Bauera rubioides, none of which is faithful to this nodum. The tree Eucalyptus urnigera and the shrub Hakea epiglottis are characteristic species for the nodum. Although their frequencies of occurrence are only moderate (58 and 71% respectively), they are uncommon elsewhere. Constant, but not faithful, species include Eucalyptus coccifera (generally forming the tallest stratum) and the graminoids Astelia alpina, Empodisma minus and Poa gunnii.

10.3.3.7 Nodum 5 : Epacris serpyllifolia - Orites acicularis - Gleichenia alpina

Nodum 5 typifies the vegetation in a similar altitudinal range to nodum 15 (i.e. 1000 to 1150m), but under somewhat poorer drainage conditions. In terms of both habitat and vegetation, nodum 5 is intermediate to 15 and 3.

Structurally, the community represented is generally open-scrub or dwarf open-forest, with the height of the tall shrub or small tree stratum ranging from 1 to 5m. Emergent eucalypts up to 10m in height sometimes occur, but with a cover of less than 10%. Mean total cover is 162%, the reduction relative to nodum 15 being largely due to the poor development of the tall tree layer.

The constant dominants are the shrubs Epacris serpyllifolia and Orites acicularis and the fern Gleichenia alpina, none of which can be considered faithful. In fact, the only species which attains its highest frequency in nodum 5 is the diminutive sedge Scirpus aucklandicus. The tall shrub/small tree stratum is typically composed of Orites acicularis and Leptospermum lanigerum. Other constant, but not faithful, species include the shrubs Baeckea gunniana, Boronia citriodora, Orites revoluta and Bauera rubioides, the graminoids Astelia alpina, Diplarrena latifolia, Empodisma minus and Poa gunnii and the herb Rubus gunnianus.

10.3.3.8 Nodum 12 : Epacris serpyllifolia - Richea scoparia - Astelia alpina

Both nodum 12 and nodum 16 represent the vegetation of moderately drained sites from about 1150 to 1260m in altitude. The vegetational differences between these two noda have been tentatively interpreted in terms of firing history. It is postulated that nodum 12 typifies sites which have been burnt within the relatively recent past (say 100 to 200 years ago), while nodum 16 exemplifies sites which have remained free of fire for a considerable length of time. This interpretation is based on the lower frequency and cover of the fire-sensitive and slow growing conifers in nodum 12. The soils of both noda are generally less than 20cm in depth, with a highly organic surface layer or shallow peat.

Structurally, the communities of nodum 12 are open-heaths in which the shrub stratum varies from 0.3 to 1m in height. The distribution of shrubs is usually patchy, with isolated individuals, or groups of individuals, separated by open areas with a well developed ground layer.

The constant dominants are the shrubs Epacris serpyllifolia and Richea scoparia and the lily Astelia alpina, none of which is faithful to the nodum. Other constant components of the shrub stratum are Helichrysum backhousii, Olearia ledifolia, Orites acicularis, O. revoluta and Richea sprengelioides. The prostrate, mat-forming shrub Pentachondra pumila, the graminoids Poa gunnii and Oreobolus acutifolius and the herbs Celmisia longifolia, Erigeron stellatus, Euphrasia striata and Rubus gunnianus are relatively constant members of the ground layer. The coniferous shrub Microstrobos niphophilus occurs in 75% of quadrats, in the form of isolated, individual bushes.

10.3.3.9 Nodum 16 : Microstrobos niphophilus - Astelia alpina

Nodum 16 is thought to typify sites with a similar physical environment to nodum 12, but which have remained free of fire for a considerable length of time. The structural form is generally closed-heath or closed-scrub, with the height of the shrub canopy ranging from 0.5 to 1.5m. On sites which have escaped firing for an exceptionally long time and which are topographically protected from the prevailing winds, the community may take the form of dwarf open-forest or dwarf woodland, with pyramidal trees of the conifer Athrotaxis cupressoides up to 4m in height.

Constant dominants are Microstrobos niphophilus and Astelia alpina, the former attaining its highest mean cover in this nodum. The coniferous shrub Diselma archeri is somewhat more frequent in nodum 16 than in noda 17 and 19, its other main centres of occurrence, and its mean cover in nodum 16 is far higher than elsewhere. Similarly, the coniferous tree Athrotaxis cupressoides reaches its highest mean cover in this nodum, although its frequency is low (14%).

Constant shrubs include Drimys lanceolata, Epacris serpyllifolia, Orites acicularis, O. revoluta, Richea scoparia and R. sprengelioides. The ground layer is less well developed than in nodum 12, probably due to the lower light intensity below the closed shrub canopy.

10.3.3.10 Nodum 11 : Cyathodes dealbata

Nodum 11 typifies the vegetation of moderately drained sites at altitudes from about 1260 to 1360m. The soils are usually very shallow (less than 10cm), with a highly organic or peaty surface. The structural form of the community is generally open-heath or low shrubland, with isolated, often wind-pruned, bushes from 0.3 to 0.5m in height.

The constant dominant is the prostrate, mat-forming shrub Cyathodes dealbata, which is characteristic of this nodum. The prostrate conifer Microcachrys tetragona is also characteristic. Other constant, but not faithful, components of the well developed ground layer are the prostrate shrub Pentachondra pumila, the herbs Celmisia saxifraga and Gentianella diemensis and the graminoids Astelia alpina, Carpha alpina, Oreobolus acutifolius and Poa gunnii. Constant members of the erect shrub stratum are Bellendena montana, Helichrysum backhousii, Orites acicularis, O. revoluta and Richea spengelioides.

10.3.3.11 Nodum 20 : Nothofagus cunninghamii - Eucryphia milliganii - Trochocarpa cunninghamii

Noda 20, 18 and 13 all encompass well drained sites in the altitudinal range 950 to 1100m. They form a compositional series, represented by axis 4 of the DCA ordination (Figure 10.3), which has been tentatively related to firing history. Nodum 20 represents the "fire protected" extreme of this gradient. The soils of all three noda are yellow-brown soils (Dimmock 1961; see section 6.4), developed over solifluction deposits or glacial moraines. The surface cover of

boulders may be as high as 70%.

The communities represented by nodum 20 are low closed-forests, sometimes with an emergent stratum of eucalypts. The closed canopy of rainforest trees varies in height from 5 to 10m, while the emergent eucalypts can be up to 25m in height.

The constant dominants are the rainforest trees Nothofagus cunninghamii ("myrtle") and Eucryphia milliganii ("leatherwood"), and the shrub Trochocarpa cunninghamii. Of these, E. milliganii may be regarded as faithful to the nodum. Other components of the rainforest tree stratum are Atherosperma moschatum and the conifers Athrotaxis cupressoides, A. selaginoides and Phyllocladus asplenifolius. Constant shrubs include Coprosma nitida, Cyathodes straminea, Drimys lanceolata, Orites diversifolia, Richea pandanifolia, R. scoparia and Telopea truncata. The climbing shrub Prionotes cerinthoides is faithful to nodum 20, although its low frequency in the data set resulted in its exclusion from the numerical analyses. The ground layer includes the herbs Oxalis lactea and Senecio leptocarpus and the ferns Blechnum wattsii and Polystichum proliferum. There is usually a well developed carpet of bryophytes. Epiphytic lichen communities abound on the trunks and stems of the rainforest trees and the larger shrubs.

10.3.3.12 Nodum 18 : Eucalyptus coccifera - Nothofagus cunninghamii - Bauera rubioides

Nodum 18 is thought to typify the intermediate region of a firing history gradient on well drained sites between 950 and 1100m in altitude. The structural form is generally open-forest or woodland, with the dominant tree stratum ranging from 10 to 25m in height.

The tall tree stratum is generally dominated by Eucalyptus coccifera, sometimes in admixture with E. subcrenulata or, less commonly, E. urnigera. Nothofagus cunninghamii usually forms a broken subordinate tree layer beneath the Eucalyptus canopy, often in combination with Leptospermum lanigerum. Constant components of the shrub stratum are Coprosma nitida, Cyathodes straminea, Drimys lanceolata, Orites diversifolia, Telopea truncata and Trochocarpa thymifolia. The scrambling shrub Bauera rubioides is constant dominant of the ground layer, with the herbs Lagenophora stipitata, Oxalis lactea and Gonocarpus serpyllifolius and the grass Deyeuxia monticola being moderately frequent.

10.3.3.13 Nodum 13 : Eucalyptus coccifera - Bauera rubioides

Nodum 13 typifies the vegetation of well drained sites between 950 and 1100m, which are at the "fire prone" extreme of the hypothesised firing history gradient. The structural form is generally open-forest or woodland, with the height of the tall tree stratum ranging from 10 to 20m. There is a subordinate tree stratum 3 to 5m in height, a low shrub stratum up to 1m in height and an open ground layer.

The constant dominant of the tall tree layer is Eucalyptus

coccifera, sometimes in admixture with either Eucalyptus subcrenulata or E. urnigera. The subordinate tree stratum generally includes Leptospermum lanigerum and Hakea lissosperma, with Banksia marginata being less frequent. Constant shrubs are Bauera rubioides, Coprosma nitida, Cyathodes parvifolia and the prostrate species Exocarpos humifusus and Monotoca empetrifolia, the latter being faithful to this nodum. Also constant and faithful to nodum 13 is the sub-shrub Olearia erubescens. The shrub Monotoca submutica var. autumnalis and the herb Stylidium graminifolium are faithful, though infrequent.

10.3.3.14 Nodum 2 : Eucalyptus coccifera - Bauera rubioides - Richea sprengelioides

Nodum 2 typifies the vegetation of well drained sites in the altitude range 1100 to 1200m. Soils are similar to those of noda 20, 18 and 13. The structural form of the community is usually woodland or low open-forest, with the tree stratum varying in height from 5 to 10m. Subordinate trees and tall shrubs are poorly represented, though there is a dense layer of low shrubs, up to 1m in height, and a sparse ground stratum. The mean number of erect shrubs reaches its maximum value of 13.9 species per sample in this nodum.

The constant dominant of the tree layer is Eucalyptus coccifera. Constant components of the shrub stratum are Bauera rubioides, Coprosma nitida, Drimys lanceolata, Orites revoluta and Richea sprengelioides. The graminoids Astelia alpina and Poa gunnii and the herb Gonocarpus serpyllifolius are fairly frequent members of the ground layer.

10.3.3.15 Nodum 10 : Richea sprengelioides - Orites revoluta

Nodum 10 typifies the vegetation of well drained sites at altitudes between 1200 and 1300m. It may be regarded as the higher altitude equivalent of nodum 2. Soils are generally rocky lithosols, less than 20cm in depth. The communities represented are open-heaths, with the height of the shrub stratum varying from 0.3 to 1m.

The shrubs Richea sprengelioides and Orites revoluta are always present and they generally dominate in terms of cover. Both species attain their highest mean cover in this nodum. Other constant members of the shrub stratum are Helichrysum backhousii, Olearia ledifolia, Coprosma nitida and Drimys lanceolata. Of moderate frequency and high mean cover are Cyathodes petiolaris, Epacris serpyllifolia and Leptospermum rupestre. The firstmentioned is a joint faithful species of this nodum and nodum 8 (comprising boulderfield sites in the same altitudinal range). Constant components of the open ground layer are Astelia alpina, the grasses Hierochloe redolens and Poa gunnii, the herb Celmisia longifolia and the prostrate shrub Pentachondra pumila.

10.3.3.16 Nodum 9 : Helichrysum backhousii - Astelia alpina - Archeria serpyllifolia

This nodum represents well drained sites in the altitude range 1300 to 1370m. The soils are lithosols, often less than 10cm in depth. Structurally, the vegetation is open-heath, with the height of the shrub stratum ranging from 0.3 to 1m.

The constant dominants are the shrubs Helichrysum backhousii, and

Archeria Serpyllifolia and the lily Astelia alpina. Both shrubs attain their highest mean cover in this nodum. Other constant shrubs are Orites acicularis and Richea sprengelioides. The coniferous shrub Diselma archeri, though occurring in only 39% of quadrats, sometimes attains a cover of 10-30%, presumably on sites which have escaped firing. Shrubs of moderate constancy include Bellendena montana, Coprosma nitida, Drimys lanceolata, Orites revoluta and Olearia ledifolia. In addition to Astelia alpina, the grasses Danthonia fortuna-hibernae and Hierochloe redolens, the herbs Gentianella diemensis and Rubus gunnianus and the prostrate shrub Pentachondra pumila are the most constant components of the ground layer. Both Astelia alpina and Helichrysum backhousii attain particularly high cover in situations subject to prolonged snow-lie, the extensive mats of the former acting as a seed-bed for the latter. The prostrate shrub Gaultheria depressa, largely faithful to this nodum, is most commonly found in these snow-patch situations. The lilies Milligania lindoniana and M. johnstonii are also associated with snow-patches.

10.3.3.17 Nodum 7 : Eucalyptus coccifera - Cyathodes parvifolia

Nodum 7 typifies the vegetation of boulderfields and screes in the altitudinal range 900 to 1050m. The structural form is open-forest or woodland, with the tree stratum varying from 10 to 25m in height. Eucalyptus coccifera is the constant dominant of the tree stratum, with E. subcrenulata being subdominant in about 50% of stands. The constant dominants of the shrub layer are Cyathodes parvifolia, Coprosma nitida and Drimys lanceolata. Other constant shrubs include Olearia phlogopappa and O. pinifolia, the former attaining its highest frequency

in this nodum. The herbs Cardamine heterophylla and Geranium potentilloides and the grass Deyeuxia monticola are all most frequent in nodum 7, the last two being constant. They are the most characteristic components of an open ground layer, occupying small accumulations of soil in rock crevices. Of relatively low frequency (30-50%), but reaching their highest mean cover and/or frequency in this nodum are the shrubs Aristotelia penduncularis and Cyathodes glauca and the tree species Atherosperma moschatum and Pittosporum bicolor, occurring as multi-stemmed shrubs. In fire protected situations, the conifer Athrotaxis selaginoides, the deciduous shrub Nothofagus gunnii and the palm-like shrub Richea pandanifolia may occur.

10.3.3.18 Nodum 1 : Eucalyptus coccifera - Nothofagus cunninghamii - Cyathodes straminea

This nodum represents the vegetation of boulderfields and screes between about 1050 and 1130m in altitude. The structural form of the community is open-forest or woodland, the height of the tree stratum ranging from 10 to 25m.

There are few floristic differences between this nodum and the lower altitude nodum 7. The separation of the noda is due to changes in the frequency of occurrence and mean cover of species. Constant dominant of the tree stratum in nodum 1 is Eucalyptus coccifera. Nothofagus cunninghamii is also constant, though generally occurring as a multi-stemmed shrub, less than 5m in height. The shrubs Cyathodes straminea and Trochocarpa cunninghamii are constant, and they often dominate the low shrub layer. Other constant shrubs are Coprosma nitida, Cyathodes parvifolia, Drimys lanceolata and Olearia pinifolia.

Most characteristic members of the open ground layer are the herbs Lagenophora stipitata and Oxalis lactea, with the graminoids Astelia alpina, Deyeuxia monticola and Hierochloe redolens being constant, but not faithful.

10.3.3.19 Nodum 4 : Eucalyptus coccifera - Drimys lanceolata

Nodum 4 typifies the vegetation of boulderfields and screes in the altitudinal range 1130 to 1220m. The structural form is woodland or dwarf woodland, the height of the tree canopy ranging from 3 to 10m.

Eucalyptus coccifera is the constant dominant of the tree layer. The shrub stratum is usually dominated by Drimys lanceolata and/or the conifer Podocarpus lawrencii. Other constant shrubs are Coprosma nitida, Cyathodes straminea and Olearia pinifolia. The most frequent components of the ground layer are the herb Rubus gunnianus, the grasses Deyeuxia monticola and Hierochloe redolens, and the prostrate shrub Exocarpos humifusus.

10.3.3.20 Nodum 8 : Podocarpus lawrencii

This nodum represents the vegetation of boulderfields and screes between about 1220 and 1310m in altitude. The usual structural form of the community is open-heath or low shrubland, with the height of the shrub stratum ranging from 0.2 to 0.8m. Average values of percentage dominance (37%) and Simpson's index (0.15) are unusually low, indicating a tendency for cover to be shared evenly among species, rather than concentrated into a few dominants.

Constant shrubs, in order of mean cover, are Podocarpus lawrencii,

Richea sprengelioides, Helichrysum backhousii, Orites acicularis, Drimys lanceolata, Orites revoluta and Olearia ledifolia. Of intermediate frequency (50-80%) are Cyathodes petiolaris, C. straminea, Epacris serpyllifolia, Richea scoparia and Trochocarpa cunninghamii. The graminoids Astelia alpina and Hierochloe redolens are the most constant components of the open ground layer.

10.3.3.21 Nodum 21 : Archeria serpyllifolia

Nodum 21 typifies the vegetation of screes and boulderfields from 1310 to 1370m in altitude. The structural form is low shrubland or low open-shrubland, the height of the shrub stratum ranging from 0.2 to 0.3m. Mean total cover is only 24%, and the mean alpha diversity is 11 species per 100m^2 sample. In contrast to nodum 8, mean values of percentage dominance (72%) and Simpson's index (0.42) are unusually high, reflecting the strong dominance of the shrub Archeria serpyllifolia.

The only other constant member of the shrub stratum is Coprosma nitida. Podocarpus lawrencii is present in about 40% of quadrats, and may attain a cover of up to 10%. Other shrubs of low constancy (less than 50%) are Olearia ledifolia, Orites revoluta, Richea scoparia and R. sprengelioides. Faithful but infrequent components of the ground layer, occurring in sheltered crevices between boulders, are the herbs Cheesemannia radicata, Epilobium gunnianum and Ourisia integrifolia. The graminoids Astelia alpina and Hierochloe redolens are constant members of the ground layer.

10.4 General Conclusion

The present study illustrates the value of an integrated approach to the descriptive analysis of vegetation. The combination of direct and indirect gradient analyses and classification has provided insights into the nature of the vegetation of the Mt. Field Plateau, and underlying environmental relationships, which could not have been gained if the analysis had been restricted to only one of these approaches.

The vegetation of the Mt. Field Plateau forms a compositional continuum, largely in relation to the two major environmental gradients, represented in the present study by altitude and drainage. The other major source of compositional variation appears to be firing history. There are no marked compositional discontinuities, corresponding with the boundaries of structural formations or the dominance-types delimited in previous classifications of the vegetation of the region (Jackson 1974; Davies 1978). Classification is useful for the purposes of synoptic description and mapping, but the boundaries between the recognised classes are essentially arbitrary.

APPENDICES

APPENDIX A : SURVEY OF ORDINATION METHODS

The following descriptions of ordination techniques are intended to provide an introduction, for those unfamiliar with the methodology. In addition, they are a source of references to works containing more detailed descriptions and other useful background material. The methods described include those which have been most widely used in plant ecology, such as Polar Ordination and Principal Components Analysis, as well as some recently introduced and less well known techniques. The account is by no means exhaustive, however all methods included in the present comparative study are described.

A.1 Polar Ordination

Polar ordination (PO) was devised by Bray and Curtis (1957) and is also known as Wisconsin comparative ordination. PO has been widely used in plant ecology, particularly in North America. Detailed descriptions have been provided by Greig-Smith (1964), Mueller-Dombois and Ellenberg (1974), Orloci (1978a) and Cottam, Goff and Whittaker (1978). Gauch (1973b) performed a quantitative evaluation of the performance of PO using data derived from Gaussian coenocline models. The conceptual basis of the method is simple. Units (e.g. stands, releves, species) are arranged according to their computed similarities to chosen pairs of end-point units, or poles. Each ordination axis is thus defined by a different pair of units. The technique shall first be described in the form originally presented. Subsequent modifications and extensions will then be outlined.

The first step involves the computation for each pair of stands of

an appropriate similarity coefficient based on their species compositions. For this purpose Bray and Curtis (1957) chose "percentage similarity", a quantitative modification of the Sorensen (1948) "coefficient of community", which is often expressed as

$$C = \frac{2w}{(a+b)} \times 100 \qquad (A1)$$

where "a" is the sum of the abundances of all species in one stand, "b" is a similar total for the other stand and "w" is the sum of the lesser scores for those species present in both stands. Values of C range from zero, when two stands have no species in common, to 100 when each possesses the same set of species in the same amounts. The computed similarities are next converted to dissimilarities by subtracting them from some fixed maximum value. Bray and Curtis (1957) used a value of 80, since empirical trials indicated a mean similarity between replicate samples of the same stand of about 82 percent.

In selecting end-points for the first (X) axis, a pair of stands is sought for which the computed similarity is minimal. Care is taken to avoid choosing as end-points outlier stands which are highly dissimilar to all others. Bray and Curtis (1957) suggested that two stands with a computed similarity of zero should only be used as end-points if each has a similarity greater than zero with every other stand. The chosen points (A and B, say) are drawn at opposite ends of a line whose length (L) is the complement of their similarity.

Suppose that the complements of the similarities between a given stand (C) and each of the two polar stands (A and B) are dA and dB

respectively. The intersection point of an arc of radius dA centred at A and one of length dB centred at B is determined and projected perpendicularly onto the X axis to obtain the X co-ordinate of stand C.

When co-ordinates on the X axis have been determined for all stands it may be found that some pairs of stands located close together on the X axis are nevertheless quite dissimilar in terms of their calculated similarity. In that case a second (Y) axis can be constructed using such a pair as reference stands. Projections of stands onto the Y axis are determined in a similar manner to that described for the X axis. The X and Y axes thus obtained are not strictly perpendicular in most cases, although scatter diagrams are generally prepared as if they were. Bray and Curtis (1957) considered that the amount of uncertainty associated with the similarity estimates did not justify the expenditure of effort necessary to correct for non-perpendicularity. Further axes can be extracted if necessary using a similar approach.

Modifications to the basic procedure were soon suggested. Beals (1960) replaced the graphical technique for locating units along axes with an equation and later presented a formula which attempts to correct for non-perpendicularity of the X and Y axes when plotting scatter diagrams (Beals 1965). Orloci (1974b, 1978a) has since provided a more rigorous method of correcting for oblique axes.

Various criteria have been used to aid in the selection of suitable reference stands. Beals (1960) chose that stand whose sum of similarities with all others was minimal as one pole for the X axis. The stand least similar to this one was then selected as the other pole.

Swan and Dix (1966) and Newsome and Dix (1968) specified criteria aimed at avoiding the selection of "outliers" or deviant samples as ordination poles, and ensuring that reference stands for the Y axis were located near the middle of the X axis. An alternative criterion based on the "negative correlation tendency" of stands was described by van der Maarel (1969). Maycock and Curtis (1960) selected as ordination poles pairs of stands corresponding to the extremes of recognised environmental gradients. This practice has been followed in numerous subsequent applications and has been recommended as the most reliable approach by Gauch (1973b).

In converting similarities to "distances", Beals (1960) followed the original authors in subtracting them from a "replicate similarity", derived by repeated sampling of the same stands. Swan and Dix (1966) and van der Maarel (1969) subtracted similarities from 100, the maximum possible value, whereas McIntosh and Hurley (1964) used Cmax-C, where Cmax is the maximum value actually obtained between any pair of stands. Bannister (1968) found that the use of Cmax-C as opposed to 100-C had little effect on the resulting ordinations in his study. However, Austin and Orloci (1966) criticised the use of such complements as dissimilarity measures in PO. The method of deriving stand positions along axes assumes that the dissimilarity measure is a metric, but functions such as 100-C or Cmax-C are not metrics. Orloci (1974b) described a number of metric functions suitable for use in PO. One of them, the relativised absolute value function, was shown to be equivalent to 2(1-C/100), where C is the percentage similarity coefficient defined by equation (A1), computed from relativised data (i.e. stand totals are all adjusted to unity). Most workers in the

"Wisconsin school" of J.T. Curtis did in fact use relativised data (Cottam, Goff and Whittaker 1978).

The computer program ORDIFLEX, which is part of the Cornell Ecology Programs Series (Gauch 1979) includes options for PO, using either user defined reference stands or pairs of stands chosen automatically by methods similar to those suggested by Bray and Curtis (1957). It also allows stands which are at the extremes of ordination axes produced by other techniques to be used as reference stands for PO.

Two ordination techniques which may be regarded as extensions of PO are the "simple ordination" of Orloci (1966, see also Austin and Orloci 1966) and the "best possible stand-defined ordination" of Swan, Dix and Wehrhahn (1969). Both are based on the use of the Euclidean distance metric as a measure of dissimilarity between the units to be ordinated. The methods described by Gauch and Whittaker (1972b) as "importance projection" and "similarity projection" are also best viewed as varieties of PO.

A.2 Principal Components Analysis

Principal Components Analysis (PCA) was originally devised by Pearson (1901) and was first applied by the psychologist Hotelling (1933). The method was introduced to plant ecology by Goodall (1954a), but widespread application was delayed until the mid 1960's, primarily because of the lack of availability of suitable computing facilities. Since then it has become established as probably the most widely used ordination technique in ecology. Adequate descriptions of the conceptual basis of PCA have been provided by a number of authors (e.g.

Seal 1964; Orloci 1966, 1978a; Pielou 1977; Noy-Meir 1971; van Groenewoud 1965; Chardy, Glemarec and Laurec 1976).

Fundamental to PCA is the conception of samples (e.g. quadrats, releves) as points in a multidimensional space, with an axis corresponding to each species represented in the set of samples. The co-ordinate of the jth sample on the ith species axis, Xij, is simply the quantity (abundance, performance) of the ith species in the jth sample. The dissimilarity between two samples is expressed as the Euclidean distance between the points representing them in this "species space". The Euclidean distance, Djk, between a pair of samples j and k is given by

$$Djk = \sqrt{\sum (Xij - Xik)^2} \qquad (A2)$$

where Xij is the abundance of species i in sample j, Xik is the abundance of species i in sample k and the summation is over all p species represented in the set of samples.

The objective of PCA is the efficient representation of the distances between every pair of points in the lowest possible dimensionality. This is achieved by moving the origin of the co-ordinate system to the centroid of the point configuration (i.e. the point whose co-ordinate on each species axis is the mean abundance of that species over all samples), then rigidly rotating the reference axes so that the first is aligned in such a direction that the squared projections onto it of the distances between each point and the centroid is maximised. Geometrically the co-ordinates of the points on this "first principal axis" represent the distances between all pairs of

points as accurately as it is possible to do so in one dimension. The second principal axis is aligned in the direction of next greatest scatter about the centroid, with the constraint that it must remain perpendicular to the first axis. Third and subsequent axes are oriented in directions accounting for successively smaller fractions of the total variability. The configuration of points on the first k principal axes represents the distances between all pairs of units as accurately as it is possible to do so in k dimensions.

Algebraically PCA involves the extraction of the eigenvalues and associated eigenvectors of a matrix of cross-products between species (the R-algorithm) or samples (the Q-algorithm). Details of the computations are given by Seal (1964), Orloci (1978a), Noy-Meir (1971) and van Groenewoud (1965). There was some confusion in the literature of the 1960's over the relationship between the R- and Q-algorithms (see Noy-Meir and Whittaker 1977). These were shown to be formally equivalent by Gower (1966). Efficient subroutines for eigenanalysis are available at all modern computing centres, making the programming of PCA a relatively trivial task. Standard statistical packages such as GENSTAT (Nelder et al. 1977) and SPSS (Nie et al. 1975) include facilities for PCA.

The eigenvalue associated with each principal axis is the sum of the squared distances from the origin of the projections of the sample points onto that axis. The sum of the eigenvalues on the first k axes, expressed as a percentage of the total sum of squared distances of samples from the origin, is a measure of the proportion of the total variability or scatter in the sample configuration accounted for by the ordination on the first k axes.

Various adjustments may be made to the data before computation of the cross-products matrix. The informal description given above assumed one such adjustment, namely the translation of the origin to the centroid of the configuration. This is achieved by adjusting the values for each species such that their mean is zero. Such a process of "centring by species" has been implicit in most applications of PCA in ecology. Orloci (1966) showed that failure to centre by species leads to a trivial first principal axis which extends from the zero origin to the centroid of the point swarm. Consequently, the subsequent axes do not reflect the major directions of variation within the point configuration. However, Noy-Meir (1971, 1973) found that non-centring can be advantageous when the data consists of two or more disjunct or partially disjunct sub-sets (i.e. groups of samples with few, if any, species in common). In such cases non-centred PCA enables an assessment of the number and sharpness of discontinuities and also minimises interference between axes representing variation within sub-sets (see also Feoli 1977).

Standardisations represent another class of adjustments which may be performed on the data prior to PCA. The use of the correlation matrix between species in R-type PCA involves an implicit standardisation, by which the values for each species are adjusted to a variance of unity. The theoretical and practical implications of data standardisations in PCA (and other numerical methods which manipulate Euclidean cross-products) were considered by Noy-Meir, Walker and Williams (1975). They concluded that the choice of a particular standardisation is essentially a decision on the a priori weightings to

be given to each sample and species in the overall analysis.

Orloci (1966, 1978a) developed a technique called "position vectors ordination" which produces ordinations approximating PCA solutions under certain circumstances, but does not require as much computation. This advantage would appear to have largely disappeared with the advent of modern computing facilities and software.

A.3 Principal Co-ordinates Analysis

Principal Co-ordinates Analysis (PCoA) can be regarded as a generalisation of PCA, which permits the use of non-Euclidean, even non-metric, measures of similarity between units. The technique was developed by Gower (1966, 1967) and has been described by Pielou (1977) and Orloci (1978a), the latter author preferring the name "principal axes analysis".

Given a matrix A, whose element aij is the computed similarity between units i and j, PCoA derives an ordination in which the Euclidean distances between units are related to the input similarities by

$$Dij = \sqrt{aii + ajj - 2aij} \qquad (A3)$$

where Dij is the distance between units i and j. When the similarity measure is defined in such a manner that self-comparisons are unity (i.e. aii=ajj=1) this reduces to

$$Dij = \sqrt{2\ (\ 1 - aij\ )} \qquad (A4)$$

Algebraically, PCoA involves the computation of the eigenvalues and associated eigenvectors of a matrix α, derived from A by performing

certain adjustments (see Gower 1966). If the coefficient in matrix A is not a metric some of the eigenvalues will be negative, indicating that a representation entirely within real space which accords exactly with equation (A3) cannot be found. However, if the moduli of the negative eigenvalues are relatively small, they appear to have little effect on the accuracy of the representation of inter-point distances by the real axes. The ordination of the units on the first k principal axes represents the inter-point distances which accord with equation (A3) as closely as is possible using k dimensions. As in PCA, the axes are orthogonal and account for successively smaller fractions of the total variability.

Like PCA, PCoA is relatively easy to program given the wide availability of efficient subroutines for eigenanalysis. Facilities for PCoA are included in statistical packages such as GENSTAT (Nelder et al. 1977).

A.4 Reciprocal Averaging

The technique introduced to plant ecology as Reciprocal Averaging (RA) by Hill (1973) is also known as correspondence analysis, an abbreviated translation of the name "Analyse Factorielle des Correspondances" used by Benzecri (1969). The method has a complex history (see Hill 1974) and it appears to have been rediscovered several times. It was originally developed by Hirschfield (1935) and independently by Fisher (1940) for the analysis of contingency tables. Later it was found to be useful as a method of multidimensional scaling (Guttman 1941; Torgerson 1958). Descriptions of RA in the ecological context are given by Hill (1973) and Orloci (1978a), both of whom

present worked examples.

RA produces dual ordinations of species and samples (quadrats, releves) which are such that the sample scores on a given axis are weighted averages of the scores on that axis of the species which occur in them. Reciprocally, the species scores are weighted averages of the scores of the samples in which they occur. The method is thus conceptually related to the simple weighted averages procedure used, for example, by Whittaker (1956, 1960) to order sites along topographic moisture gradients and by Curtis and McIntosh (1951) to place stands in a forest continuum. One algorithm for RA does involve an iterative process, whereby sample scores obtained as weighted averages of a trial set of species scores are used to derive improved species scores. These are, in turn, used to compute new sample scores. The back-and-forth averaging process eventually converges to a unique solution, regardless of the trial species scores used initially. Further ordination axes can be obtained by correcting for axes already extracted at each iteration (see Hill 1973).

It can easily be shown, however, that RA is essentially an eigenanalysis problem (Hill 1973, 1974) and may be regarded, together with PCA and PCoA, as a special case of a general "inertia method" (Chardy, Glemarec and Laurec 1976), which attempts to summarise the relationships between points by a configuration of reduced dimension. Implicit in RA is a simultaneous double standardisation of each value in the data matrix by the totals of the row (species) and column (sample) in which it occurs. If Xij represents the abundance of species i in sample j, Si represents the total abundance over all samples of species

i and Qj represents the total abundance of all species in sample j, then RA effectively operates on standardised data given by Xij/(Si.Qj). However, RA differs from a PCA of such standardised data, in that species and samples are given weights equal to their totals (S and Q in the above terminology) in computing the cross-products. Chardy, Glemarec and Laurec (1976) show that this amounts to a conceptualisation of samples as points with co-ordinates Xij/(√Si.Qj). The distance, Djk, between two samples, j and k, is given by

$$Djk = \sqrt{\sum \frac{1}{Si} \left(\frac{Xij}{Qj} - \frac{Xik}{Qk} \right)^2} \qquad (A5)$$

where the terms have the same meanings as defined above and the summation extends over all p species recorded in the samples. This distance measure has been called the "Chi-squared distance" (Benzecri et al. 1973). The statement by Hill and Gauch (1980) that RA "makes no use of the concept of compositional distance" is misleading.

The computer programs ORDIFLEX (Gauch 1977) and DECORANA (Hill 1979a), both part of the Cornell Ecology Programs Series, include options for RA.

A.5 Detrended Correspondence Analysis

Detrended Correspondence Analysis (DCA) is a modified version of RA. It was developed by Hill (Hill and Gauch 1980) in an attempt to overcome two undesirable features of RA which are apparent in RA ordinations of data from simple models representing a single floristic gradient. These are the so-called "arch effect", whereby sample (and species) scores on the second axis bear an approximately quadratic

relationship to those on the first axis, and the tendency for the distances between samples to be compressed towards the extremes of the first axis, even though the compositional differences between samples are equal in all parts of the underlying gradient. Hill and Gauch (1980) provide an example which illustrates these two effects.

DCA attempts to eliminate the arch effect by detrending sample scores on each axis with respect to those on each previously extracted axis during each iteration of a two-way averaging algorithm. For example, when computing scores on the second axis the first axis is divided into segments and second axis scores are adjusted so that their (weighted) mean in each segment is zero. For third and subsequent axes, the detrending is carried out individually with respect to each previously extracted axis. Hill and Gauch (1980) point out that this does not eliminate the possibility that a given axis may have a strong curvilinear relationship with some combination of previous axes.

DCA also incorporates a rescaling procedure which attempts to equalise the mean within-sample dispersion of species scores at all points along an axis. This tends to counteract the tendency for samples to be compressed towards the ends of the axes. Details are given by Hill (1979a). Hill and Gauch (1980) note that, for models in which the abundance profiles of species along a gradient are Gaussian in form, this rescaling adjusts the average standard deviation of the Gaussian response curves to unity. In such cases the lengths of the axes produced by DCA are effectively expressed in the "Z" units of Gauch and Whittaker (1972a).

The computer program DECORANA (Hill 1979a), which is part of the

Cornell Ecology Program Series, performs the computations necessary for DCA. It is particularly efficient in terms of both memory usage and speed.

A.6 Non-metric Multidimensional Scaling

The group of related techniques collectively known as Non-metric Multidimensional Scaling (NMDS) have their origins in the work of psychologists such as Shepard (1962a,b) and Kruskal (1964a,b). Descriptions of the techniques are given by Kruskal (1964a) and, in an ecological context, by Fasham (1977), Prentice (1977) and Clymo (1980).

Given a matrix representing the similarities between pairs of units (e.g. quadrats, releves, species) NMDS attempts to find a configuration of points in a metric space of specified dimensionality, such that the distances between points in this configuration are, as far as possible, in the same rank order as the input similarities. The epithet "non-metric" derives from the fact that only the rank orders of the input similarities are considered. This contrasts with PCoA and other methods of "metric scaling" where the relative magnitudes of the similarities are utilised.

NMDS requires the dimensionality of the ordination (i.e. the number of axes) to be specified in advance. An initial configuration specifying the starting positions of the units in the ordination must also be supplied. This may be entirely random, or the co-ordinates on the first axes of some other ordination of the units may be used. The distances between units in the ordination are then computed and their rank order is compared with that of the input similarities by fitting a

similarities appears preferable in ecological applications (Prentice 1977; Clymo 1980).

NMDS is easily adapted to handle input resemblance coefficients of the dissimilarity type. In such cases, an ascending monotone regression is used to assess the rank order agreement between ordination distances and input dissimilarities. It should be noted that, since only the rank order of the input coefficients is considered, different resemblance functions whose values over a set of units are monotonic will give identical results when employed in NMDS.

The basic method described above is the so-called "global" variant of NMDS. Global NMDS requires that the ordination distances between units should be monotonic with their similarities over all pairs of units. This can be expressed symbolically as

$$Sij > Skl \Rightarrow Dij \leq Dkl \quad \text{for all } i,j,k,l \qquad (A7)$$

where Sij is the similarity between units i and j, Dij is the ordination distance between units i and j and Skl and Dkl have similar meanings for units k and l.

In contrast, "local" NMDS (Sibson 1972) requires only that, for each unit, the distances from that unit to each other unit in the ordination are in the same rank order as the similarities between that unit and each other unit. Symbolically

$$Sij > Sik \Rightarrow Dij \leq Dik \quad \text{for all } i,j,k \qquad (A8)$$

where the notation is analogous to equation (A7). This amounts to fitting a separate monotonic regression for distances involving each unit, and using the pooled deviations from the regressions in computing

stress. Prentice (1977, 1980) has argued that local NMDS is likely to be more appropriate in ecological applications than the global form.

The iterative algorithms used in NMDS are not guaranteed always to converge to a solution with the lowest possible stress. Sometimes the method may become trapped in a "local optimum" where no small change in the point configuration will decrease stress. The likelihood of encountering such a local optimum is greatest with unidimensional ordinations. The use of a starting configuration derived from some other ordination technique, rather than a random one, should generally help to avoid problems with local optima (Fasham 1977). Confidence that the overall optimum has been achieved may be increased by performing several ordinations with different starting configurations.

Another major problem is that computing cost for NMDS increases non-linearly with the number of samples to be ordinated (Gauch, Whittaker and Singer 1981). Most current programs for NMDS can only handle about 2000 input similarities, corresponding to a total of about 65 samples. Clymo (1980) has suggested one possible method of accomodating greater numbers of samples. This involves discarding some of the similarities before analysis. Most programs for NMDS allow some of the input similarities to be coded as "missing". Obvious candidates for exclusion are the indeterminate zero similarities between samples with no species in common.

A further difficulty is the determination of the number of dimensions required for ordination. This problem has been discussed by several authors (Kruskal 1964a; Shepard 1974; Fasham 1977). Finally, the value of stress cannot be used uncritically as a measure of

ordination adequacy, since its value has been shown to depend not only on the quality of the monotonic fit between input similarities and ordination distances, but also on the number of samples, the dimensionality of the ordination and the distance metric used in the ordination (Klahr 1969; Sherman 1972; Spence 1972; Wagenaar and Padmos 1971).

Recent computer programs for NMDS include ALSCAL (Young and Lewyckyj 1979) and POLYCON (Young 1978), both of which are from the Thurstone Psychometric Laboratory. Neither of these programs can perform the local variant of NMDS. For this purpose one may use SIBSON, a program available from Professor R. Sibson at the University of Bath (see Gauch, Whittaker and Singer 1981), or one of the more flexible but older programs such as KYST (Kruskal, Young and Seery 1973), a product of the Bell Telephone Laboratories.

A.7 Parametric Mapping

Parametric Mapping was developed by the psychologist J.D. Carroll (Shepard and Carroll 1966), and was introduced to plant ecology by Noy-Meir (1974a,b), who suggested the alternative title "continuity analysis". Noy-Meir (1974a) has provided a clear description of the technique in an ecological context. The basic goal of Parametric Mapping is to derive an ordination in a specified number of dimensions, such that the observed variables (species) are related to the ordination axes by functions which are as smooth or continuous as possible, but without any constraints on the precise form of these functions.

Given an input matrix of the compositional distances between all

pairs of samples, as expressed by an appropriate metric, and an initial configuration of points representing the units in a space of specified dimensionality, Parametric Mapping seeks to minimise an index of non-continuity between the ordination distances and the input distances, by iteratively adjusting the positions of the points in the ordination. The notion of continuity, as defined in this procedure, implies that small distances in the ordination should correspond to relatively small input distances. As one moves from one point in the ordination to another point nearby, the abundances of each species should change by only a small amount, rather than in large, irregular jumps. The index of non-continuity, designated as Kappa, incorporates an "adjacency weighting" which is intended to place the emphasis on "local" continuity (see Noy-Meir 1974a). The "steepness" of the adjacency weighting is controlled by the value given to a user-defined parameter.

The only available computer program for Parametric Mapping appears to be PARAMAP (Chang 1969), which is part of a multidimensional scaling package available from the Bell Telephone Laboratories.

A.8 Gaussian Ordination

Gaussian Ordination was developed by Gauch, Chase and Whittaker (1974; see also Gauch and Chase 1974) with ecological applications in mind. Descriptions of the technique are given by Gauch, Chase and Whittaker (1974), Orloci (1978a) and Austin (1976b). Ihm and van Groenewoud (1975) presented a method with similar objectives, but a different theoretical basis involving several restrictive assumptions. This account is confined to the approach of Gauch, Chase and Whittaker (1974).

Gaussian Ordination is based on an explicit hypothesis regarding the shape of species abundance profiles along environmental gradients, namely that they are of Gaussian form. The method is able to produce only unidimensional ordinations, and hence it is not appropriate for data sets having more than one major underlying direction of compositional variation. Starting with an initial estimate of sample positions along a single axis, Gaussian Ordination uses an iterative variation of parameters approach (Gauch and Chase 1974) to fit Gaussian regressions, relating the abundance values of each species to the ordination axis. Sample scores are then adjusted, in a manner likely to improve the fit of the Gaussian regressions for all species. The entire process of fitting regressions and adjusting sample positions is iterated until either the ordination scores cease to change appreciably or the percentage of the total sum of squares accounted for by the regressions exceeds some acceptable value. The final results include not only a unidimensional ordination of the samples, but also the parameters of the Gaussian regressions for each species.

The initial estimate of sample positions is normally based on an approximate direct gradient analysis or the results of some other ordination method. Random arrangements may be used, although the convergence to a solution is then less rapid.

Since the computations involved in Gaussian Ordination are rather heavy, Gauch, Chase and Whittaker (1974) recommend prior sorting of species, deleting those which are poorly represented in the data set and ordering the remainder according to some criterion of "informativeness". Gaussian Ordination can then be commenced using only those species

ranked most highly, and the other species may be introduced after a certain number of iterations.

A computer program for Gaussian Ordination is available as part of the Cornell Ecology Program Series (Gauch 1979). Another program in the series performs the species screening and ranking just described.

A.9 Maximum Likelihood Non-linear Ordination

Johnson and Goodall (1979) described a technique for non-linear ordination based on a maximum likelihood approach. The method shall be referred to here as Maximum Likelihood Non-linear Ordination. As first proposed the technique could produce only unidimensional ordinations, although it has since been generalised to several dimensions (Goodall and Johnson 1982).

Given a starting configuration, representing the samples in a space of specified dimensionality, Maximum Likelihood Non-linear Ordination fits "bell-shaped" hypersurfaces for each species, relating both the probability of occurrence and the abundance if present to the positions of the samples in the ordination. Sample positions are then adjusted, using maximum likelihood criteria, in such a manner as is calculated to improve the fit of these regressions. New regressions are then fitted and the process iterated until stopping conditions, related to the percentage of total variance accounted for by the regressions, the rate of change in sample positions or the sums of the likelihood values are satisfied.

Maximum Likelihood Non-linear Ordination is similar in philosophy

to Gaussian Ordination, although the regressions fitted are not strictly Gaussian in form and the fitting procedures are quite different. The technique also differs from Gaussian Ordination in its ability to derive multidimensional ordinations and in the utilisation of the qualitative or presence-absence component of the species data, as well as the abundances.

Tests of the method with artificial data (Goodall and Johnson 1982) have suggested that it requires a starting configuration reasonably close to the "true" solution, in order to reduce the possibility of non-convergence or entrappment in local minima. A computer program, MAXMIN, which performs Maximum Likelihood Non-linear Ordination is available at cost from the authors.

APPENDIX B : LIST OF SPECIES

The following is an alphabetical list of those species encountered during sampling. It is not intended as a census of the vascular flora of the Mt. Field Plateau. Several species of rare or localised occurrence within the study area were not sampled, and others are known to occur outside the study area.

For each species, the following information is given: (a) the authority for the name, (b) family, (c) growth-form and (d) frequency of occurrence (%) among the 438, 100m^2 samples whose locations are shown in Figure 7.1. The meanings of the abbreviations used for growth-forms are as follows: Tr = tree, ESh = erect or ascending shrub, PSh = prostrate or mat-forming shrub, TSh = twining or climbing shrub, CSh = cushion or bolster-forming shrub, Gr = graminoid, PHe = perennial dicotyledonous herb, AHe = annual herb or geophyte, Fe = fern or lycopsid. Further notes on nomenclature are given in section 7.4.

SPECIES	AUTHORITY	FAMILY	GROWTH-FORM	FREQ. (%)
Abrotanella forsteroides	(Hook. f.) Benth.	COMPOSITAE	CSh	5.3
Abrotanella scapigera	(F. Muell.) Benth.	COMPOSITAE	PHe	1.4
Acaena montana	Hook. f.	ROSACEAE	PHe	8.9
Acaena novae-zelandiae	Kirk	ROSACEAE	PHe	4.1
Actinotus suffocata	(Hook. f.) Rodw.	UMBELLIFERAE	PHe	4.3
Agrostis parviflora	R. Br.	GRAMINEAE	Gr	2.7
Archeria comberi	Melville	EPACRIDACEAE	ESh	0.9
Archeria serpyllifolia	Hook. f.	EPACRIDACEAE	ESh	10.5
Aristotelia peduncularis	(Labill.) Hook. f.	ELAEOCARPACEAE	ESh	6.2
Asplenium flabellifolium	Cav.	ASPLENIACEAE	Fe	0.5
Astelia alpina	R. Br.	LILIACEAE	Gr	82.2
Atherosperma moschatum	Labill.	MONIMIACEAE	Tr	2.7
Athrotaxis cupressoides	D. Don	TAXODIACEAE	Tr	3.2
Athrotaxis selaginoides	D. Don	TAXODIACEAE	Tr	2.1
Baeckea gunniana	Schauer ex Walp.	MYRTACEAE	ESh	25.8
Banksia marginata	Cav.	PROTEACEAE	Tr	5.3
Bauera rubioides	Andr.	CUNONIACEAE	ESh	45.0
Bellendena montana	R. Br.	PROTEACEAE	ESh	28.1
Billardiera longiflora	Labill.	PITTOSPORACEAE	TSh	1.1
Blandfordia punicea	(Labill.) Sweet	LILIACEAE	Gr	2.1
Blechnum penna-marina	(Poir.) Kuhn	BLECHNACEAE	Fe	3.9
Blechnum wattsii	M.D. Tindale	BLECHNACEAE	Fe	1.4
Boronia citriodora	Gunn ex Hook. f.	RUTACEAE	ESh	21.0
Brachycome tenuiscapa	Hook. f.	COMPOSITAE	PHe	4.3
Campynema lineare	Labill.	HYPOXIDACEAE	AHe	4.3
Cardamine heterophylla	Hook.	CRUCIFEREAE	PHe	8.7
Carex appressa	R. Br.	CYPERACEAE	Gr	2.7
Carex breviculmis	R. Br.	CYPERACEAE	Gr	0.7
Carpha alpina	R. Br.	CYPERACEAE	Gr	42.7
Carpha sp. nov.		CYPERACEAE	Gr	3.7
Celmisia longifolia	Cass.	COMPOSITAE	PHe	48.2
Celmisia saxifraga	Comber	COMPOSITAE	PHe	7.1
Centrolepis monogyna	(Hook. f.) Benth.	CENTROLEPIDACEAE	Gr	5.0
Centrolepis sp. nov.		CENTROLEPIDACEAE	Gr	0.2
Cheesemannia radicata	(Hook. f.) O.E. Schulz	CRUCIFEREAE	PHe	1.1
Coprosma nitida	Hook. f.	RUBIACEAE	ESh	66.0
Cotula alpina	Hook. f.	COMPOSITAE	PHe	0.5
Cotula filicula	(Hook. f.) Benth.	COMPOSITAE	PHe	0.7
Craspedia alpina	Backhouse ex Hook. f.	COMPOSITAE	PHe	7.3
Cyathodes dealbata	R. Br.	EPACRIDACEAE	PSh	13.7
Cyathodes glauca	Labill.	EPACRIDACEAE	ESh	6.4
Cyathodes parvifolia	R. Br.	EPACRIDACEAE	ESh	35.4
Cyathodes petiolaris	(DC.) Druce	EPACRIDACEAE	ESh	13.7
Cyathodes straminea	R. Br.	EPACRIDACEAE	ESh	35.8
Danthonia fortuna-hibernae	Renvoize	GRAMINEAE	Gr	24.7
Danthonia nivicola	J.W. Vickery	GRAMINEAE	Gr	0.2
Danthonia pauciflora	R. Br.	GRAMINEAE	Gr	12.1
Deyeuxia carinata	J.W. Vickery	GRAMINEAE	Gr	0.9
Deyeuxia monticola	(Roem. & Schult.) J.W. Vickery	GRAMINEAE	Gr	29.2
Deyeuxia sp. nov.		GRAMINEAE	Gr	1.1

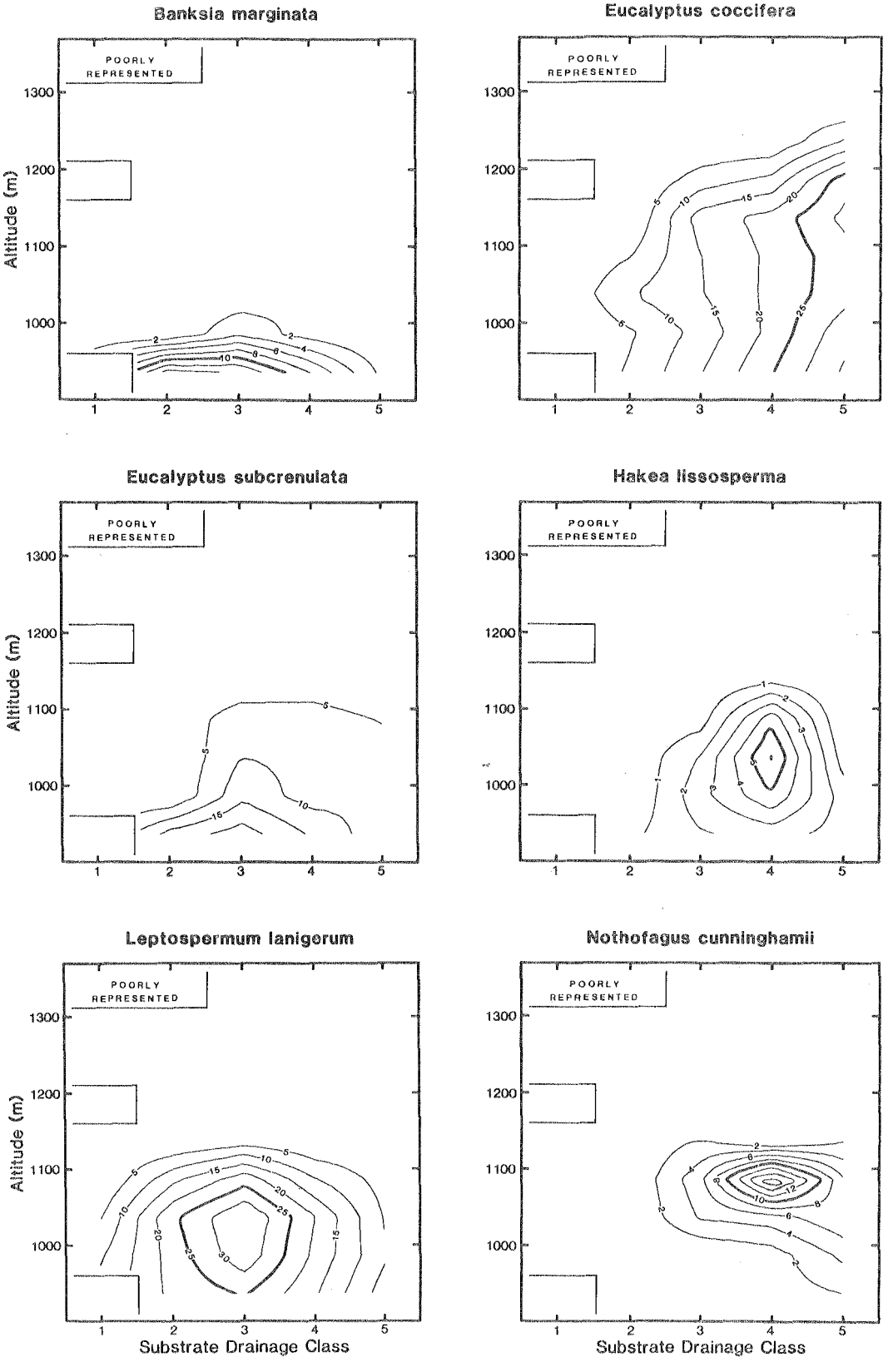
SPECIES	AUTHORITY	FAMILY	GROWTH-FORM	FREQ. (%)
Diplarrena latifolia	Benth.	IRIDACEAE	Gr	23.3
Diplaspis cordifolia	Hook. f.	UMBELLIFERAE	PHe	5.0
Diselma archeri	Hook. f.	CUPRESSACEAE	ESh	14.8
Donatia novae-zelandiae	J.R. & G. Forst.	DONATIACEAE	CSh	0.2
Dracophyllum milliganii	Hook. f.	EPACRIDACEAE	ESh	1.8
Dracophyllum minimum	F. Muell.	EPACRIDACEAE	CSh	1.6
Drimys lanceolata	(Poir.) Baill.	WINTERACEAE	ESh	71.9
Drosera arcturi	Hook.	DROSERACEAE	AHe	14.4
Drosera binata	Labill.	DROSERACEAE	PHe	0.2
Drosera pygmaea	DC.	DROSERACEAE	PHe	0.7
Empodisma minus	(Hook. f.) L.A.S. Johnson & Cutler	RESTIONACEAE	Gr	48.9
Epacris gunnii	Hook. f.	EPACRIDACEAE	ESh	0.2
Epacris impressa	Labill.	EPACRIDACEAE	ESh	0.2
Epacris lanuginosa	Labill.	EPACRIDACEAE	ESh	0.2
Epacris serpyllifolia	R. Br.	EPACRIDACEAE	ESh	68.5
Epilobium gunnianum	Hausskn.	ONAGRACEAE	PHe	2.7
Epilobium sarmentaceum	Hausskn.	ONAGRACEAE	PHe	3.2
Erigeron pappochroma	Labill.	COMPOSITAE	PHe	33.3
Erigeron stellatus	(Hook. f.) W.M. Curtis	COMPOSITAE	PHe	17.4
Eucalyptus coccifera	Hook. f.	MYRTACEAE	Tr	41.8
Eucalyptus delegatensis	R.T. Baker	MYRTACEAE	Tr	0.7
Eucalyptus gunnii	Hook. f.	MYRTACEAE	Tr	0.2
Eucalyptus subcrenulata	Maiden & Blakely	MYRTACEAE	Tr	15.8
Eucalyptus urnigera	Hook. f.	MYRTACEAE	Tr	5.7
Eucryphia milliganii	Hook. f.	EUCRYPHIACEAE	Tr	3.0
Euphrasia gibbsiae	Du Rietz	SCROPHULARIACEAE	PHe	10.0
Euphrasia striata	R. Br.	SCROPHULARIACEAE	PHe	22.6
Ewartia meridithae	(F. Muell.) Beauv.	COMPOSITAE	PHe	4.1
Ewartia planchonii	(Hook. f.) Beauv.	COMPOSITAE	PHe	6.6
Exocarpos humifusus	R. Br.	SANTALACEAE	PSh	36.3
Forstera bellidifolia	Hook. f.	STYLIDIACEAE	PHe	0.2
Gahnia grandis	(Labill.) S.T. Blake	CYPERACEAE	Gr	12.1
Gaimardia fitzgeraldi	F. Muell. & Rodw.	CENTROLEPIDACEAE	Gr	0.2
Gaimardia setacea	Hook. f.	CENTROLEPIDACEAE	Gr	0.7
Galium australe	DC.	RUBIACEAE	PHe	0.5
Gaultheria depressa	Hook. f.	ERICACEAE	PSh	2.3
Gaultheria hispida	R. Br.	ERICACEAE	ESh	14.6
Gentianella diemensis	(Griseb.) J.H. Willis	GENTIANACEAE	AHe	21.0
Geranium potentilloides	L'Herit. ex DC.	GERANIACEAE	PHe	12.3
Gleichenia alpina	R. Br.	GLEICHENIACEAE	Fe	21.5
Gnaphalium collinum var. monocephalum	Hook. f.	COMPOSITAE	PHe	2.3
Gnaphalium involucratum	Forst. f.	COMPOSITAE	AHe	0.2
Gnaphalium traversii	Hook. f.	COMPOSITAE	PHe	0.2
Gnaphalium umbricolum	J.H. Willis	COMPOSITAE	PHe	0.9
Gonocarpus serpyllifolius	Hook. f.	HALORAGACEAE	PHe	45.4
Grammitis armstrongii	M.D. Tindale	GRAMMITIDACEAE	Fe	5.5
Grammitis billardieri	Willd.	GRAMMITIDACEAE	Fe	0.5
Gymnoshoenus sphaerocephalus	(R. Br.) Hook. f.	CYPERACEAE	Gr	1.8
Hakea epiglottis	Labill.	PROTEACEAE	ESh	9.8
Hakea lissosperma	R. Br.	PROTEACEAE	Tr	9.4

SPECIES	AUTHORITY	FAMILY	GROWTH-FORM	FREQ. (%)
Helichrysum antennarium	(DC.) F. Muell. ex Benth.	COMPOSITAE	ESh	0.2
Helichrysum backhousii	(Hook. f.) F. Muell. ex Benth.	COMPOSITAE	ESh	43.8
Helichrysum backhousii var. oreophilum	W.M. Curtis	COMPOSITAE	ESh	0.2
Helichrysum hookeri	(Sond.) Druce	COMPOSITAE	ESh	9.8
Helichrysum ledifolium	(DC.) Benth.	COMPOSITAE	ESh	5.0
Helichrysum pumilum	Hook. f.	COMPOSITAE	PHe	3.7
Hierochloe redolens	(Soland. ex Vahl) Roem. & Schult.	GRAMINEAE	Gr	45.0
Histiopteris incisa	(Thunb.) J. Sm.	DENNSTAEDTIACEAE	Fe	0.7
Hydrocotyle sibthorpioides	Lamk.	UMBELLIFERAE	PHe	1.6
Hypericum japonicum	Thunb. ex Murr.	HYPERICACEAE	PHe	0.2
Juncus sandwithii	Lourteig	JUNCACEAE	Gr	0.5
Lagenophora stipitata	(Labill.) Druce	COMPOSITAE	PHe	19.4
Leontodon leysseri	(Wallr.) Beck	COMPOSITAE	PHe	0.5
Lepidosperma filiforme	Labill.	CYPERACEAE	Gr	16.0
Lepidosperma lineare var. inops	F. Muell. ex Rodw.	CYPERACEAE	Gr	3.7
Leptospermum lanigerum	(Ait.) Sm.	MYRTACEAE	Tr	28.1
Leptospermum nitidum	Hook. f.	MYRTACEAE	Tr	1.4
Leptospermum rupestre	Hook. f.	MYRTACEAE	ESh	28.1
Lepyrodia tasmanica	Hook. f.	RESTIONACEAE	Gr	0.2
Lissanthe montana	R. Br.	EPACRIDACEAE	ESh	5.5
Lomatia polymorpha	R. Br.	PROTEACEAE	ESh	14.2
Luzula campestris	(L.) DC. in Lam. & DC.	JUNCACEAE	Gr	0.2
Luzula novae-cambriae	Gandoger	JUNCACEAE	Gr	0.2
Luzula australasica ssp. australasica	Steud.	JUNCACEAE	Gr	5.5
Lycopodium australianum	Herter & Allan	LYCOPODIACEAE	Ly	8.2
Lycopodium fastigiatum	R. Br.	LYCOPODIACEAE	Ly	23.5
Lycopodium scariosum	Forst. f.	LYCOPODIACEAE	Ly	13.0
Melaleuca squamea	Labill.	MYRTACEAE	ESh	4.3
Microcachrys tetragona	(Hook.) Hook. f.	PODOCARPACEAE	PSh	15.5
Microstrobos niphophilus	Garden & Johnson	PODOCARPACEAE	ESh	25.8
Milligania densiflora	Hook. f.	LILIACEAE	Gr	0.2
Milligania johnstonii	F. Muell. ex Benth.	LILIACEAE	Gr	0.2
Milligania lindoniana	Rodw. ex W.M. Curtis	LILIACEAE	Gr	0.2
Mitrasacme archeri	Hook. f.	LOGANIACEAE	PHe	7.1
Mitrasacme montana	Hook. f.	LOGANIACEAE	PHe	12.3
Monotoca empetrifolia	R. Br.	EPACRIDACEAE	ESh	12.1
Monotoca glauca	(Labill.) Druce	EPACRIDACEAE	ESh	0.2
Monotoca submutica var. autumnalis	S.J. Jarman	EPACRIDACEAE	ESh	1.4
Nothofagus cunninghamii	(Hook.) Oerst.	FAGACEAE	Tr	11.4
Nothofagus gunnii	(Hook. f.) Oerst.	FAGACEAE	ESh	0.7
Olearia algida	N.A. Wakefield	COMPOSITAE	ESh	0.2
Olearia erubescens	(DC.) Dippel	COMPOSITAE	ESh	12.1
Olearia ledifolia	(DC.) Benth.	COMPOSITAE	ESh	45.2
Olearia obcordata	(Hook. f.) Benth.	COMPOSITAE	ESh	0.9
Olearia persoonioides	(DC.) Benth.	COMPOSITAE	ESh	3.4
Olearia phlogopappa	(Labill.) DC.	COMPOSITAE	ESh	16.9
Olearia pinifolia	(Hook. f.) Benth.	COMPOSITAE	ESh	24.0
Oreobolus acutifolius	S.T. Blake	CYPERACEAE	Gr	19.6
Oreobolus distichus	F. Muell.	CYPERACEAE	Gr	1.1
Oreobolus oxycarpus	S.T. Blake	CYPERACEAE	Gr	12.3

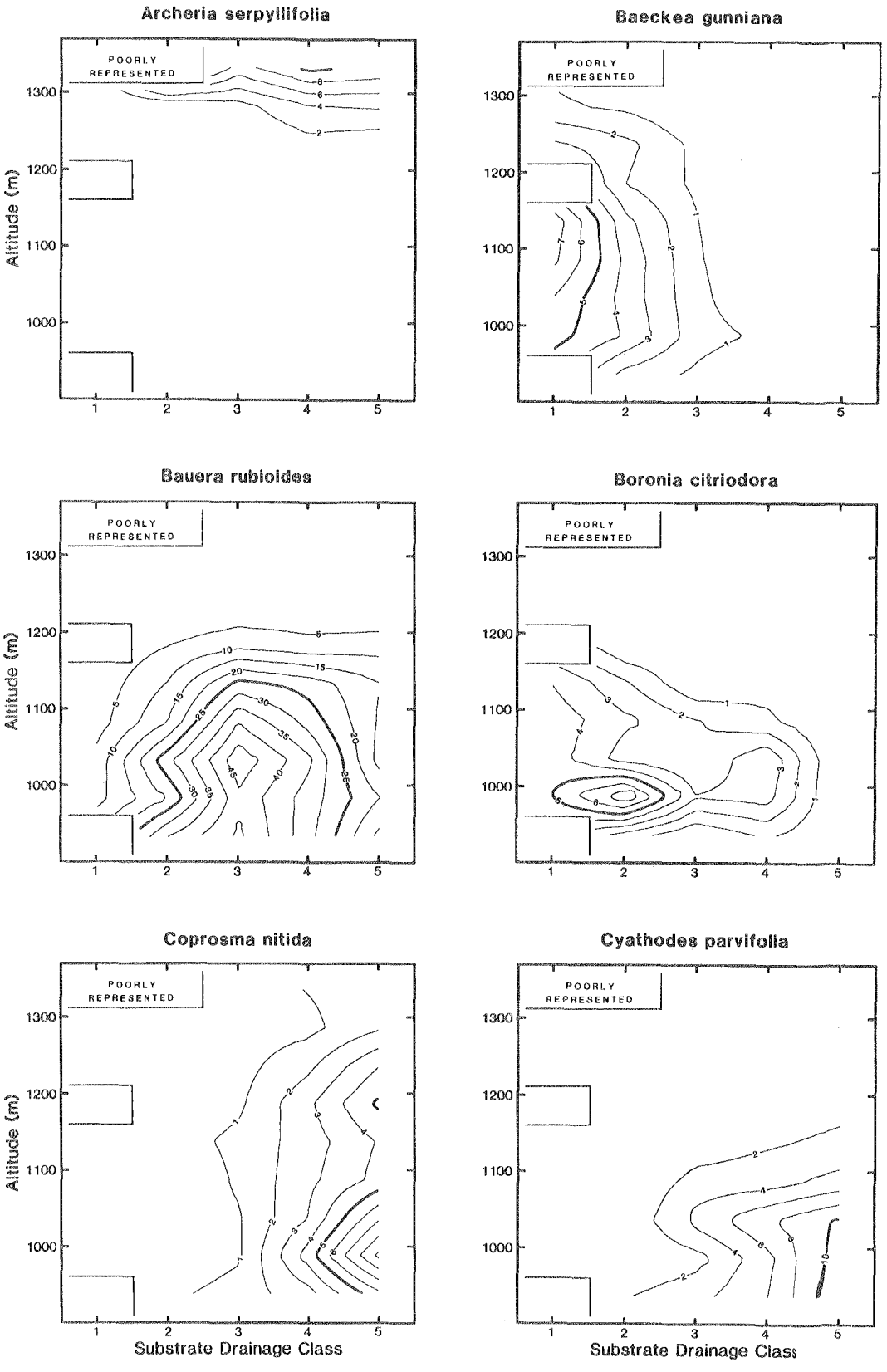
SPECIES	AUTHORITY	FAMILY	GROWTH-FORM	FREQ. (%)
Oreobolus pumilio	R. Br.	CYPERACEAE	Gr	21.0
Oreomyrrhis eriopoda	(DC.) Hook. f.	UMBELLIFERAE	PHe	0.2
Orites acicularis	R. Br.	PROTEACEAE	ESh	50.7
Orites diversifolia	R. Br.	PROTEACEAE	ESh	18.5
Orites revoluta	R. Br.	PROTEACEAE	ESh	69.2
Ourisia integrifolia	R. Br.	SCROPHULARIACEAE	PHe	2.1
Oxalis lactea	Hook.	OXALIDACEAE	PHe	8.0
Pentachondra pumila	(Forst.) R. Br.	EPACRIDACEAE	PSh	34.0
Persoonia gunnii	Hook. f.	PROTEACEAE	ESh	5.3
Phyllocladus aspleniifolius	(Labill.) Hook. f.	PODOCARPACEAE	Tr	2.1
Pimelea drupacea	Labill.	THYMELAEACEAE	ESh	1.4
Pimelea sericea	R. Br.	THYMELAEACEAE	ESh	15.1
Pittosporum bicolor	Hook.	PITTOSPORACEAE	Tr	3.4
Plantago gunnii	Hook. f.	PLANTAGINACEAE	PHe	0.7
Plantago tasmanica	Hook. f.	PLANTAGINACEAE	PHe	8.2
Poa gunnii	J.W. Vickery	GRAMINEAE	Gr	65.3
Poa saxicola	J.W. Vickery	GRAMINEAE	Gr	0.7
Podocarpus lawrencii	Hook. f. in Hook.	PODOCARPACEAE	ESh	28.1
Polystichum proliferum	(R. Br.) C. Presl	ASPIDIACEAE	Fe	8.4
Poranthera microphylla	Brogn.	EUPHORBIACEAE	PHe	0.2
Prionotes cerinthoides	(Labill.) R. Br.	EPACRIDACEAE	TSh	0.9
Pterygopappus lawrencii	Hook. f.	COMPOSITAE	PHe	4.1
Ranunculus collinus	R. Br. ex DC.	RANUNCULACEAE	PHe	0.2
Restio australis	R. Br.	RESTIONACEAE	Gr	8.9
Restio complanatus	R. Br.	RESTIONACEAE	Gr	4.1
Richea gunnii	Hook. f.	EPACRIDACEAE	ESh	4.3
Richea pandanifolia	Hook. f.	EPACRIDACEAE	Tr	10.3
Richea procera	(F. Muell.) F. Muell.	EPACRIDACEAE	ESh	0.2
Richea scoparia	Hook. f.	EPACRIOACEAE	ESh	45.4
Richea sprengelioides	(R. Br.) F. Muell.	EPACRIDACEAE	ESh	63.2
Rubus gunnianus	Hook.	ROSACEAE	PHe	53.4
Scaevola hookeri	(de Vriese) Hook. f.	GOODENIACEAE	PHe	0.5
Schizea fistulosa	Labill.	SCHIZAEACEAE	Fe	0.5
Scirpus aucklandicus	(Hook. f.) Boeck.	CYPERACEAE	Gr	14.6
Scirpus subtillisimus	(Boeck.) S.T. Blake	CYPERACEAE	Gr	0.7
Senecio gunnii	(Hook. f.) Belcher	COMPOSITAE	PHe	1.1
Senecio leptocarpus	DC.	COMPOSITAE	PHe	6.8
Senecio pectinatus var. pectinatus	DC.	COMPOSITAE	PHe	14.4
Senecio pectinatus var. ochroleuca	Rodw.	COMPOSITAE	PHe	0.5
Sprengelia incarnata	Sm.	EPACRIDACEAE	ESh	18.5
Sphagnum cristatum	Hampe	SPHAGNACEAE	??	1.4
Stylidium graminifolium	Swartz	STYLIDIACEAE	PHe	0.9
Telopea truncata	(Labill.) R. Br.	PROTEACEAE	ESh	26.7
Tetracarpaea tasmanica	Hook. f.	ESCALLONIACEAE	ESh	0.7
Tetrarrhena oreophila var. oreophila	D.I. Morris	GRAMINEAE	Gr	0.5
Tetratheca procumbens	Gunn ex Hook. f.	TREMANDRACEAE	PSh	0.5
Trochocarpa cunninghamii	(DC.) W.M. Curtis	EPACRIDACEAE	ESh	26.3
Trochocarpa thymifolia	(R. Br.) Spreng.	EPACRIDACEAE	ESh	21.9
Uncinia compacta	R. Br.	CYPERACEAE	Gr	69.6
Viola hederacea	Labill.	VIOLACEAE	PHe	3.7

APPENDIX C : ECOLOGICAL RESPONSE SURFACES FOR 54 SELECTED SPECIES

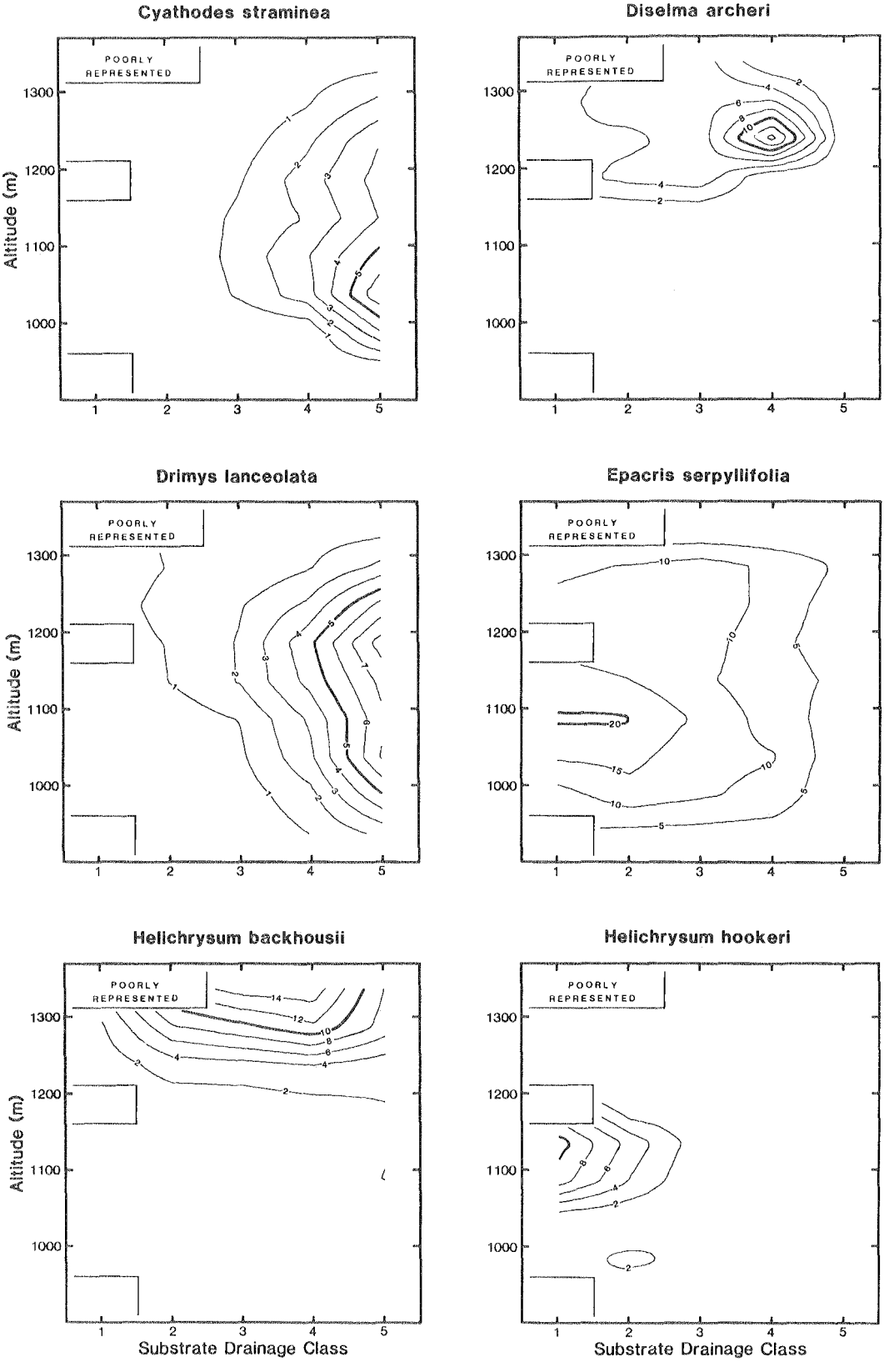
The following contour diagrams illustrate the relationships between the mean percentage cover of 54 selected species and the environmental plane defined by the altitudinal and drainage gradients. In each diagram, the contours join points of equal percentage cover on the response surface. The grids of mean cover values were smoothed by a weighted moving average procedure, before fitting the contours (see section 8.2.2). The diagrams are arranged in groups, according to growth-form.



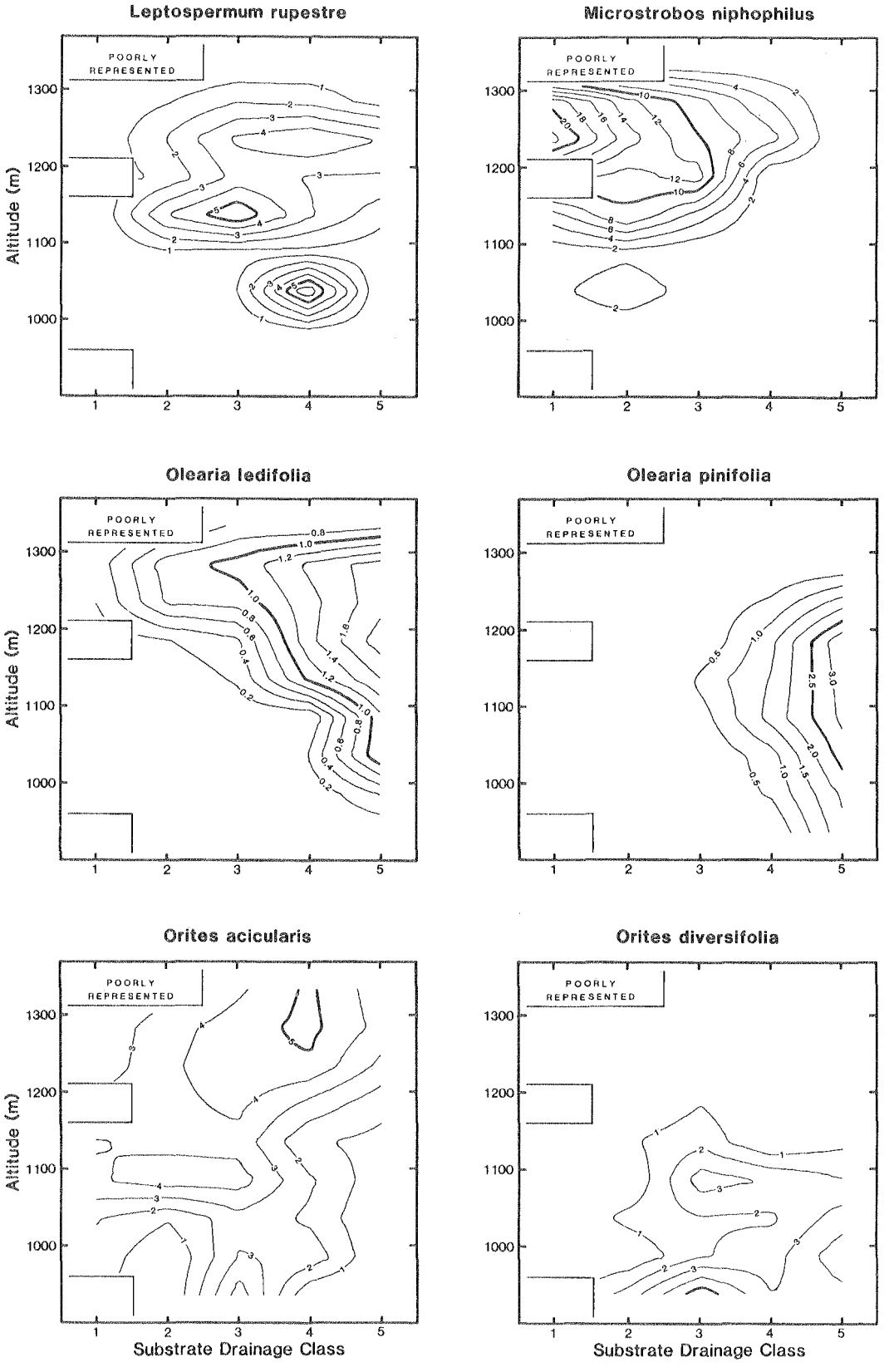
Smoothed ecological response surfaces (mean percentage cover) for selected tree species.



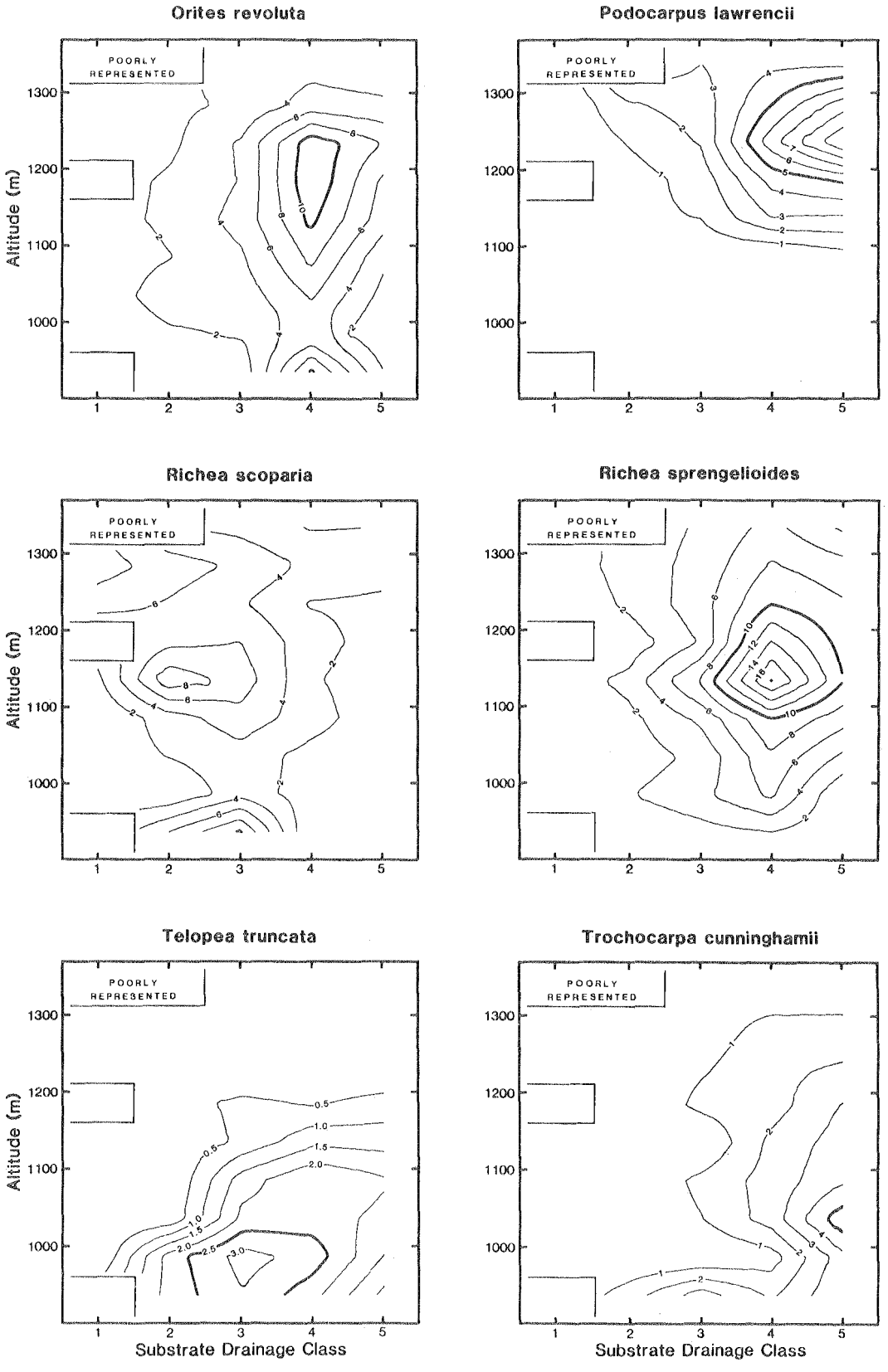
Smoothed ecological response surfaces (mean percentage cover) for selected erect or ascending shrub species.



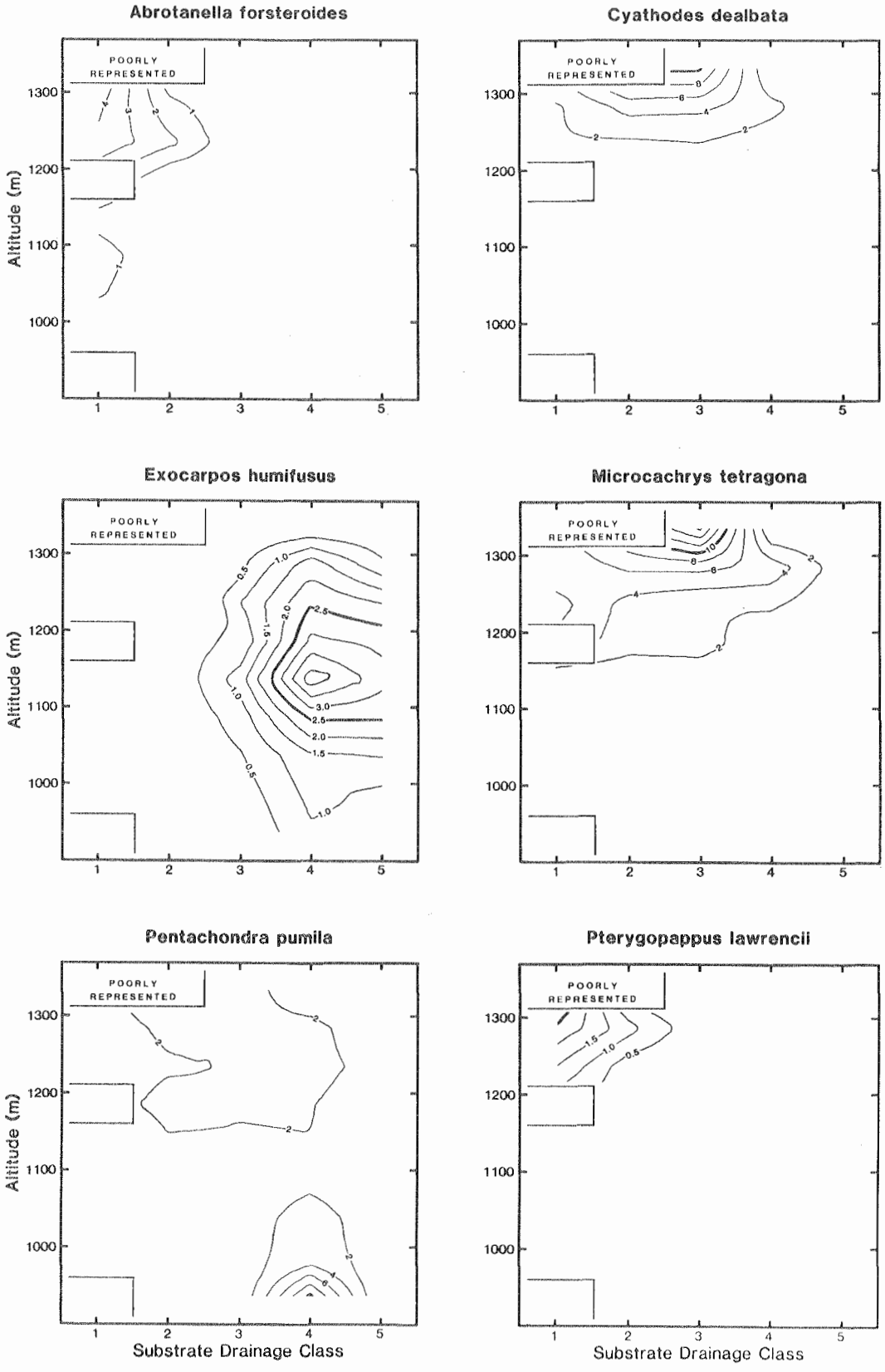
Smoothed ecological response surfaces (mean percentage cover) for selected erect or ascending shrub species (continued).



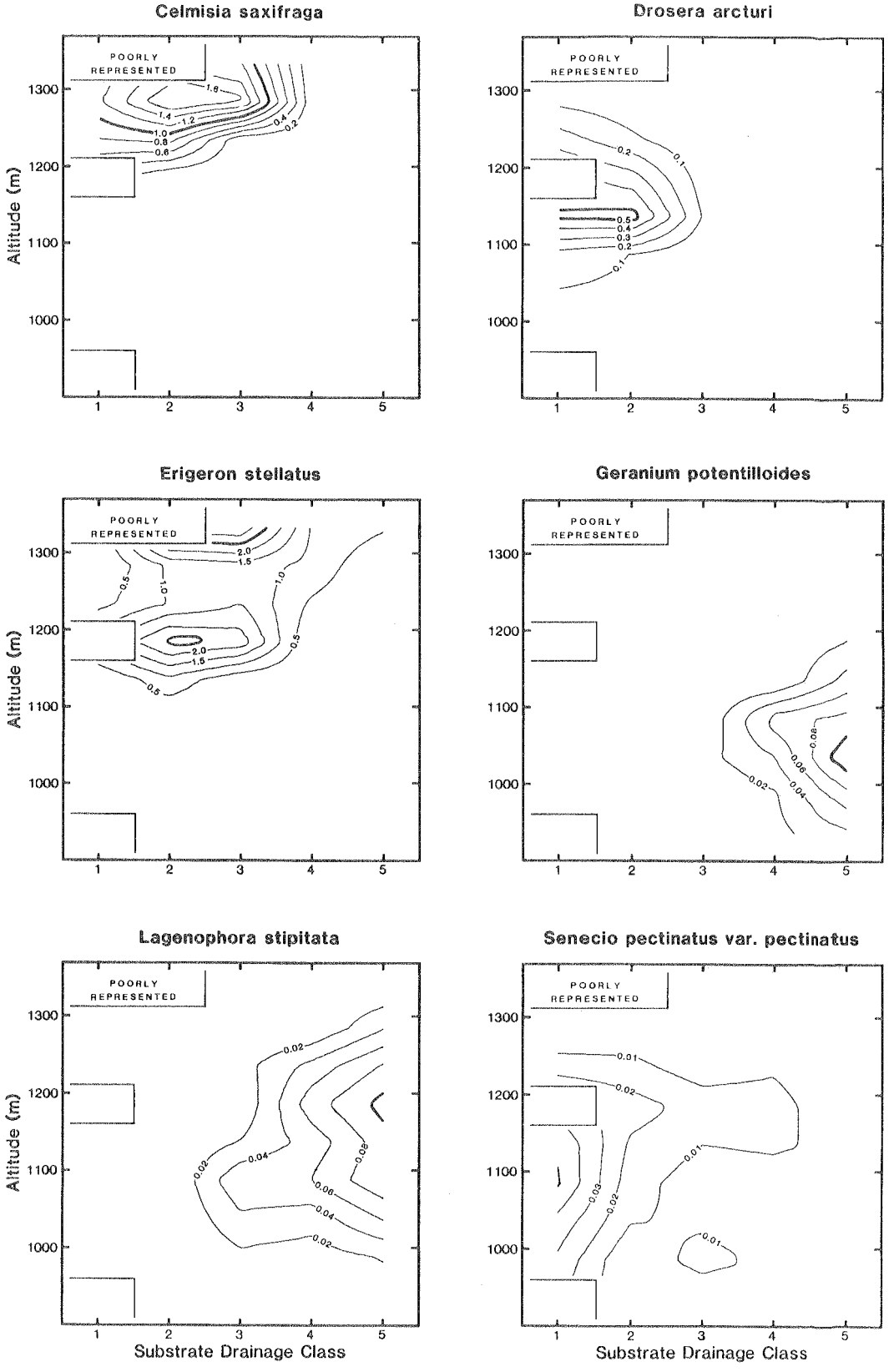
Smoothed ecological response surfaces (mean percentage cover) for selected erect or ascending shrub species (continued).



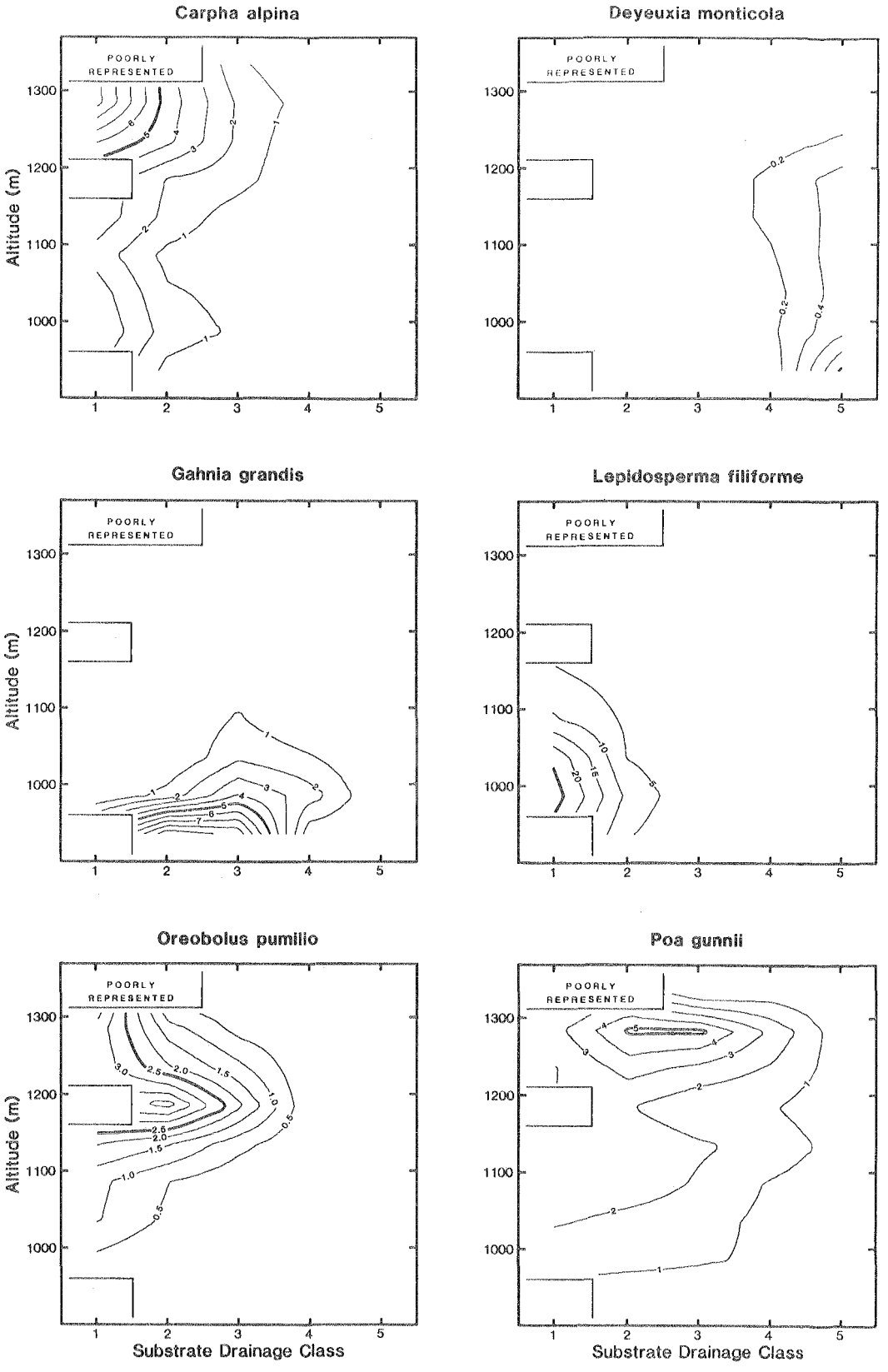
Smoothed ecological response surfaces (mean percentage cover) for selected erect or ascending shrub species (continued).



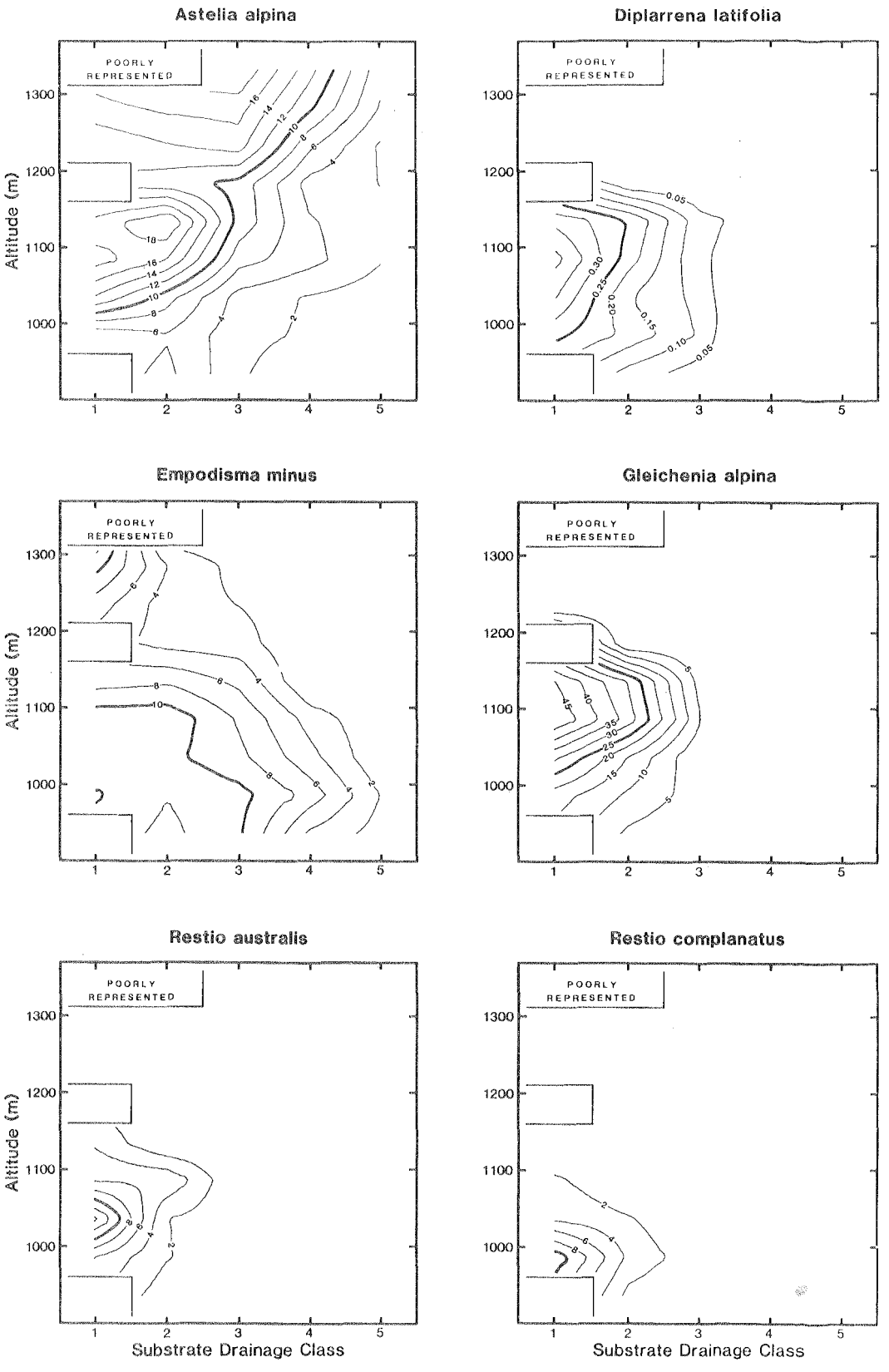
Smoothed ecological response surfaces (mean percentage cover) for selected prostrate, mat-forming or cushion-forming shrub species and a cushion-forming herb (*Pterygopappus lawrencii*).



Smoothed ecological response surfaces (mean percentage cover) for selected perennial herb species and a geophyte (*Drosera arcturi*).



Smoothed ecological response surfaces (mean percentage cover) for selected sedges and grasses.



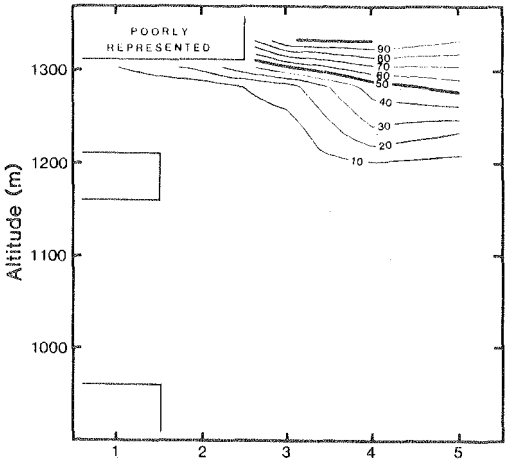
Smoothed ecological response surfaces (mean percentage cover) for selected graminoid species and a fern (*Gleichenia alpina*).

APPENDIX D : GENERALISED LINEAR MODELS FOR 18 SELECTED SPECIES

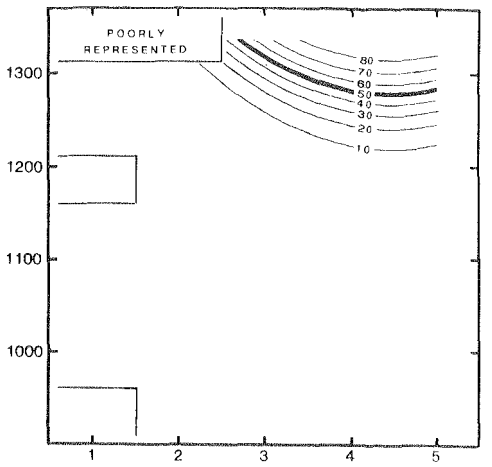
The following contour diagrams illustrate the observed and fitted response surfaces for both probability of occurrence (%) and percentage cover, for each of 18 selected species. In each diagram, the contours join points of equal probability or percentage cover. The "observed probability of occurrence" diagrams were produced without prior smoothing of the probability estimates in each grid cell. Expected probability surfaces were fitted using Generalised Linear Modelling (GLM), with a binomial error distribution and logit as a link function. In preparing the observed percentage cover diagrams. the grids of mean percentage cover values were smoothed by a weighted moving average procedure (section 8.2.2). The expected percentage cover surfaces were fitted using least-squares multiple regression, and are based on individual quadrat values, rather than cell means. The dashed line on each expected cover diagram indicates the position of the 10% probability of occurrence contour (from the fitted binomial model). Quadrats outside this contour were excluded from the cover regression. The equations of the fitted probability and cover models are given in Tables 8.8 and 8.9 respectively.

ARCHERIA SERPYLLIFOLIA

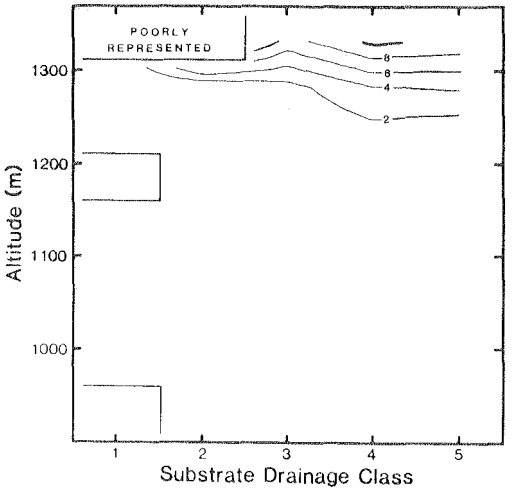
Observed Probability of Occurrence



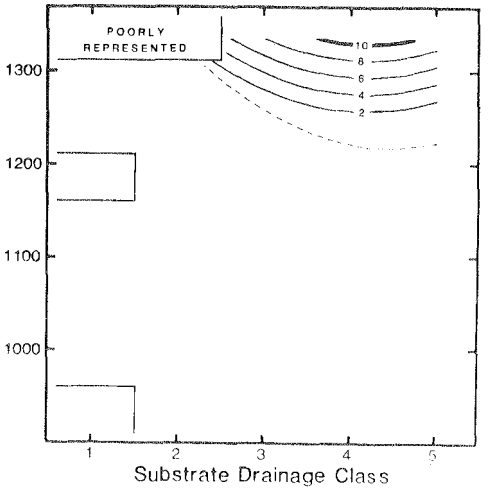
Expected Probability (from Binomial GLM)



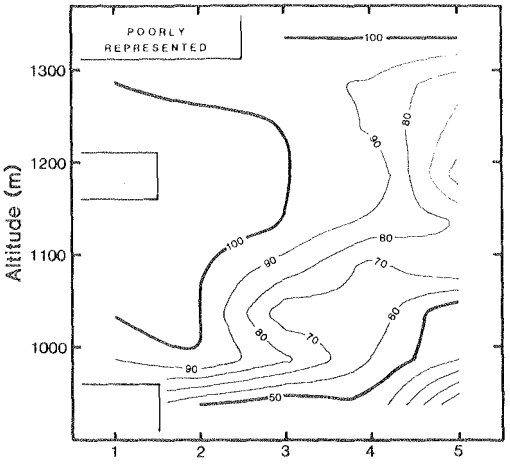
Observed Percentage Cover (Smoothed)



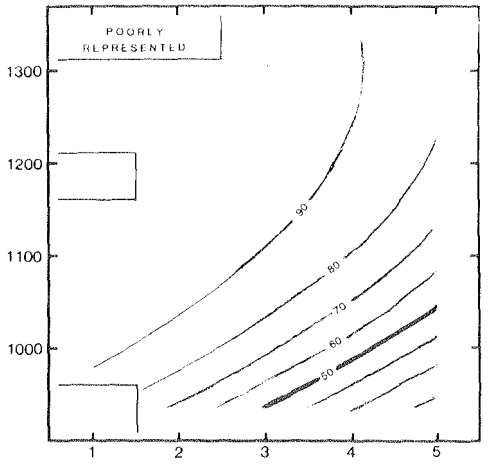
Expected Cover (from Normal Model)



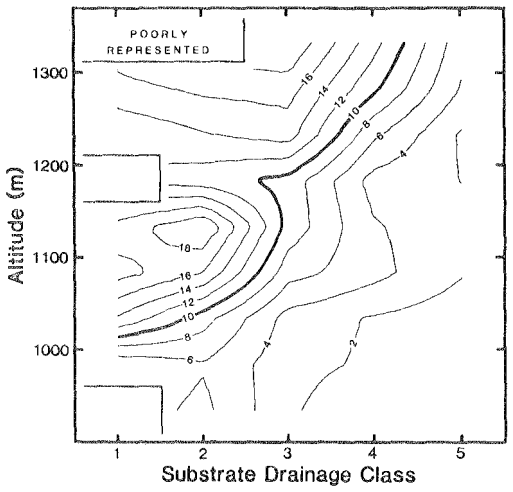
Observed Probability of Occurrence



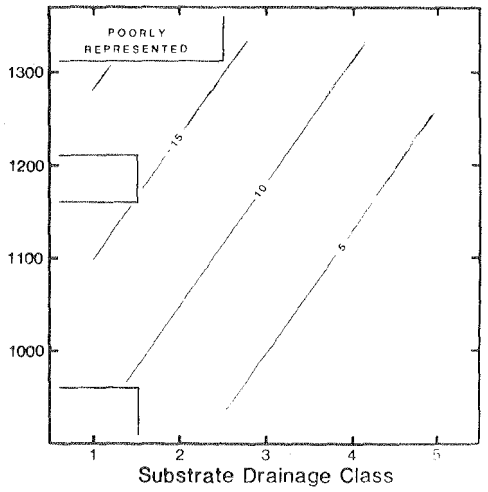
Expected Probability (from Binomial GLM)



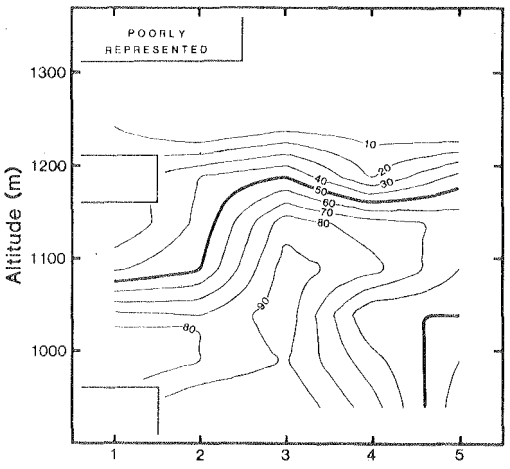
Observed Percentage Cover (Smoothed)



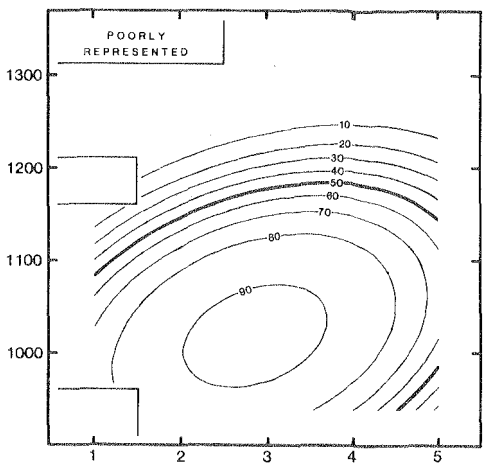
Expected Cover (from Normal Model)



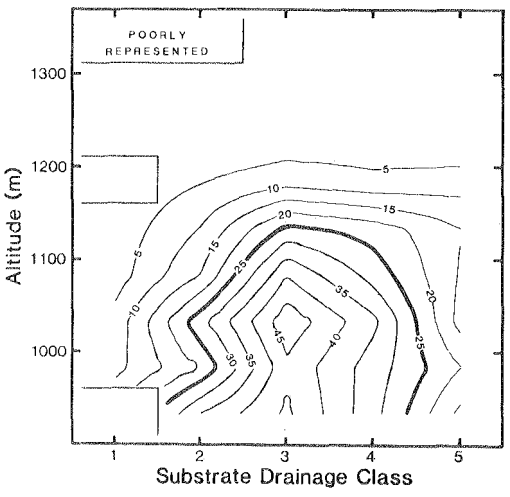
Observed Probability of Occurrence



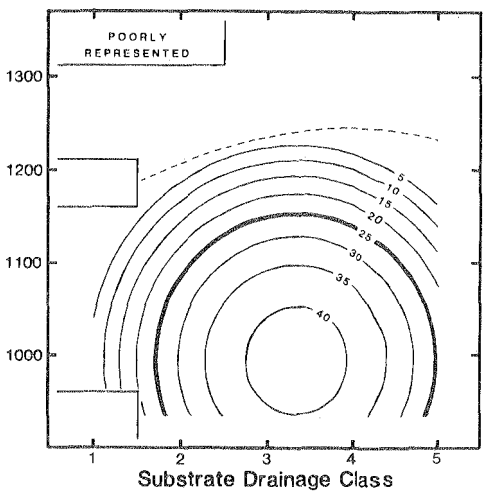
Expected Probability (from Binomial GLM)



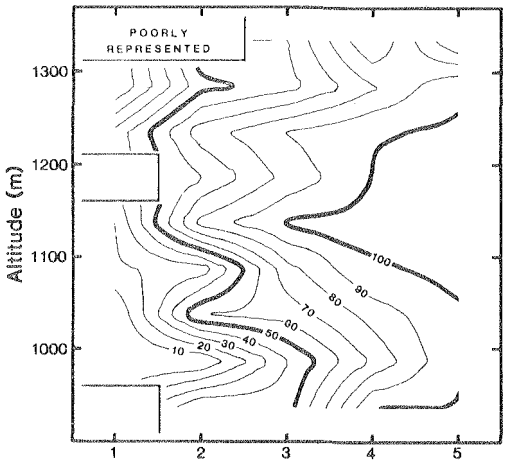
Observed Percentage Cover (Smoothed)



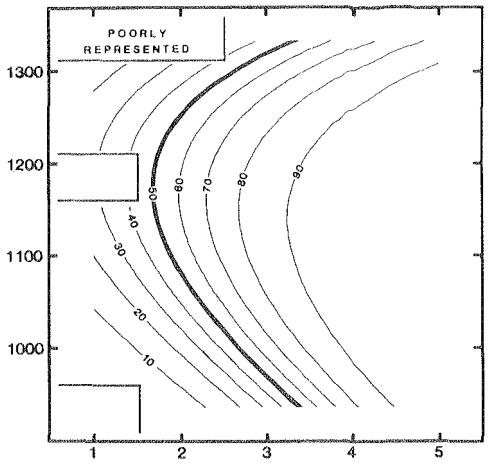
Expected Cover (from Normal Model)



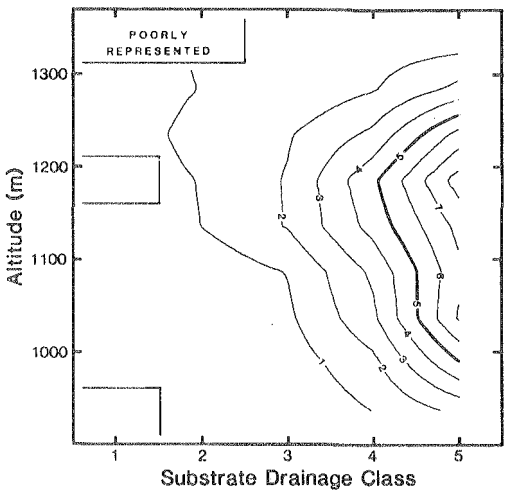
Observed Probability of Occurrence



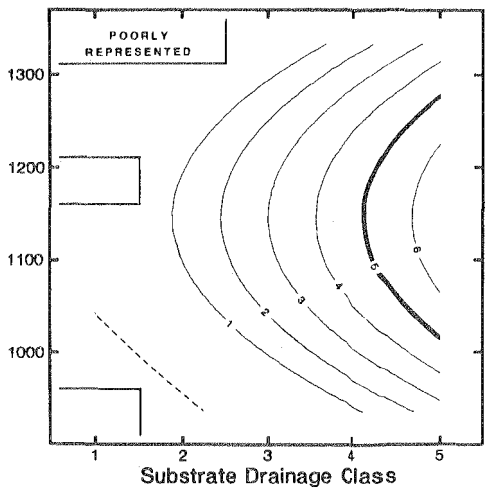
Expected Probability (from Binomial GLM)



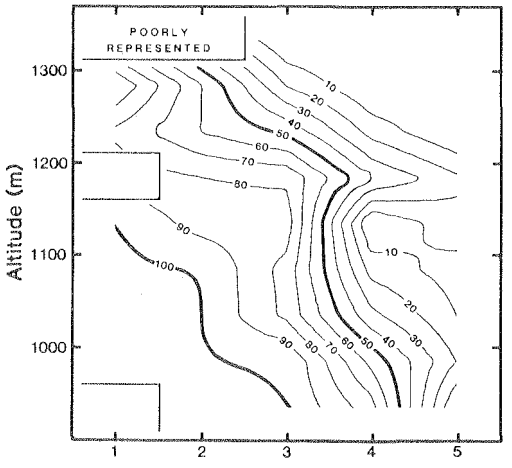
Observed Percentage Cover (Smoothed)



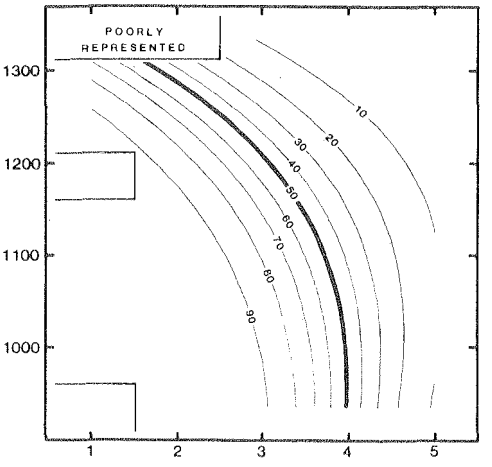
Expected Cover (from Normal Model)



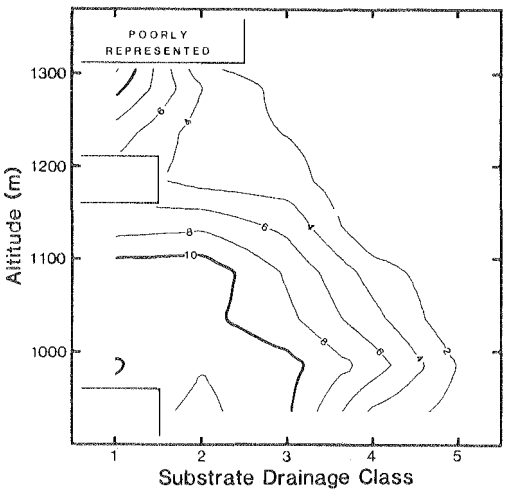
Observed Probability of Occurrence



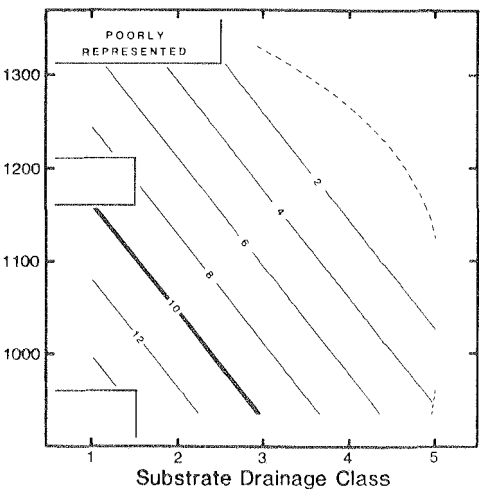
Expected Probability (from Binomial GLM)



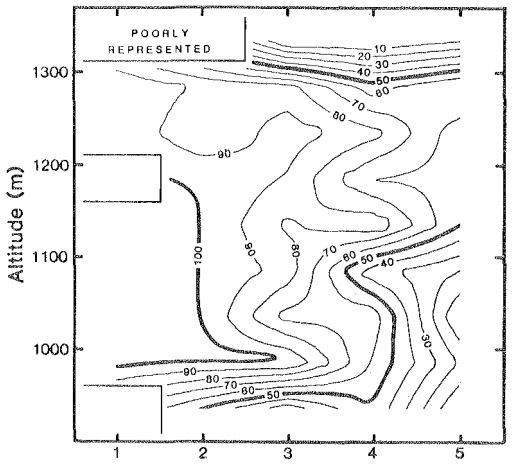
Observed Percentage Cover (Smoothed)



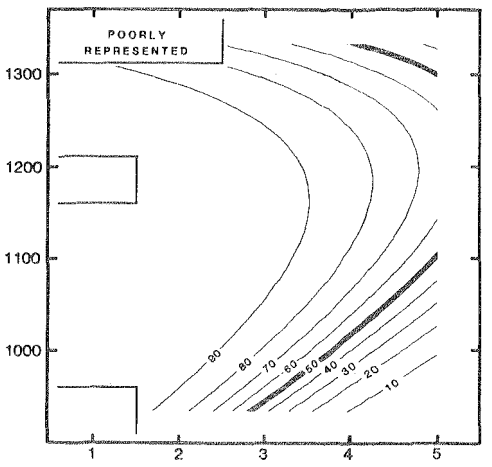
Expected Cover (from Normal Model)



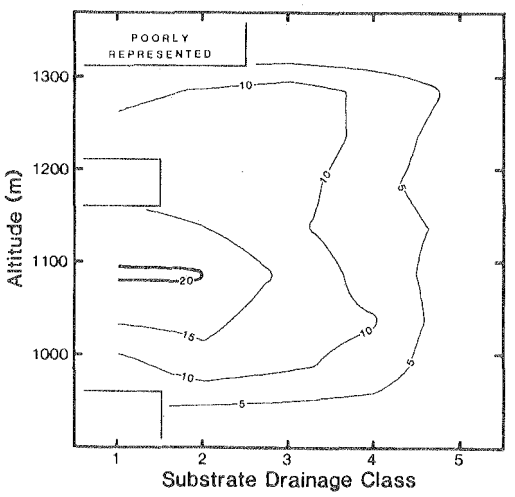
Observed Probability of Occurrence



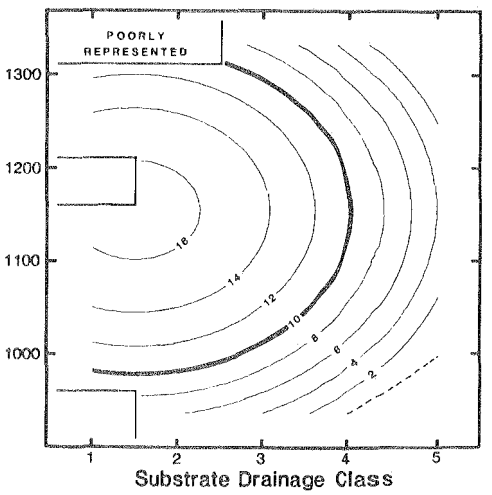
Expected Probability (from Binomial GLM)



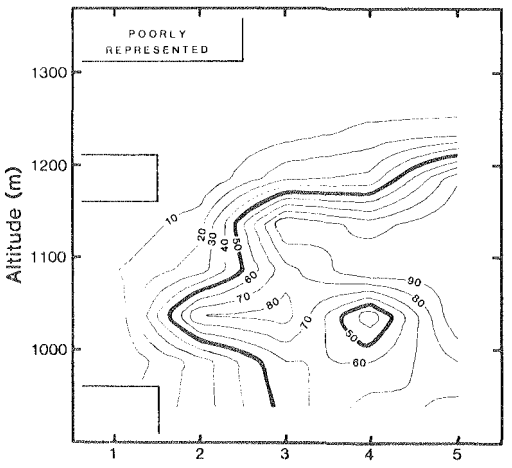
Observed Percentage Cover (Smoothed)



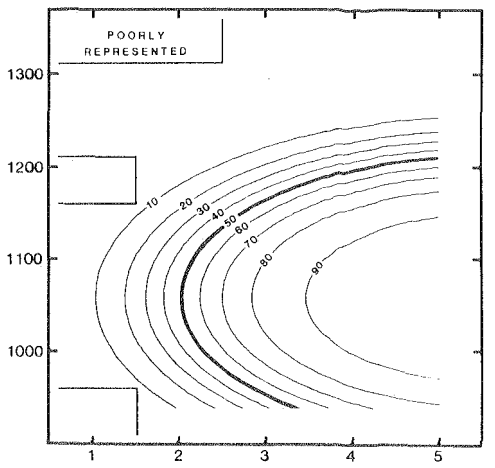
Expected Cover (from Normal Model)



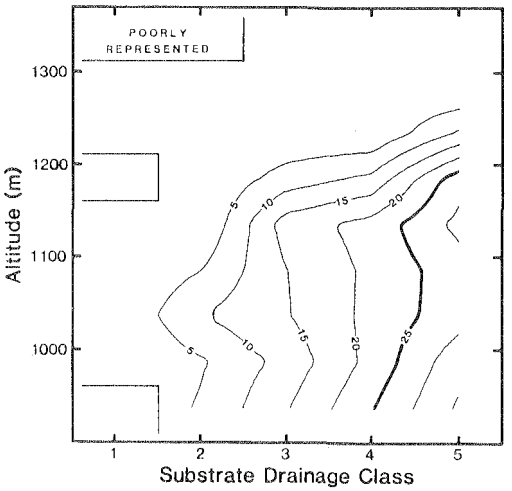
Observed Probability of Occurrence



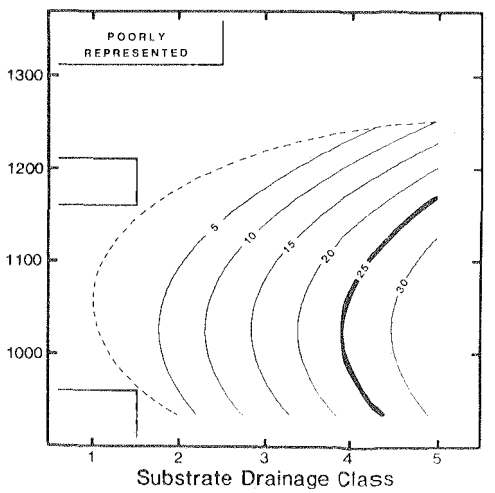
Expected Probability (from Binomial GLM)



Observed Percentage Cover (Smoothed)

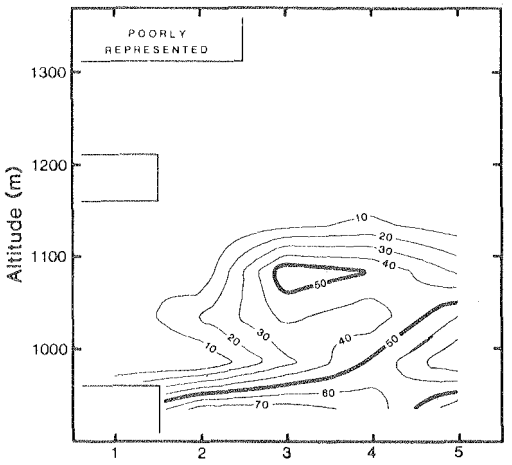


Expected Cover (from Normal Model)

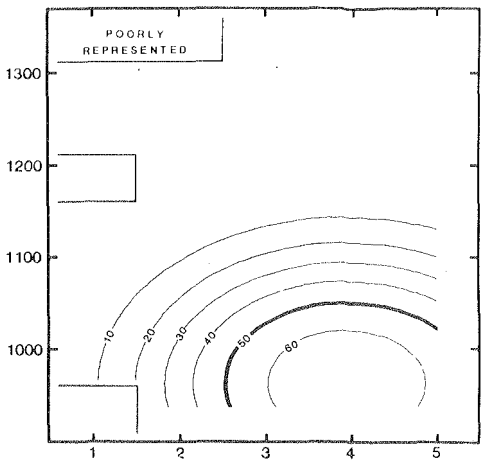


EUCALYPTUS SUBCRENULATA

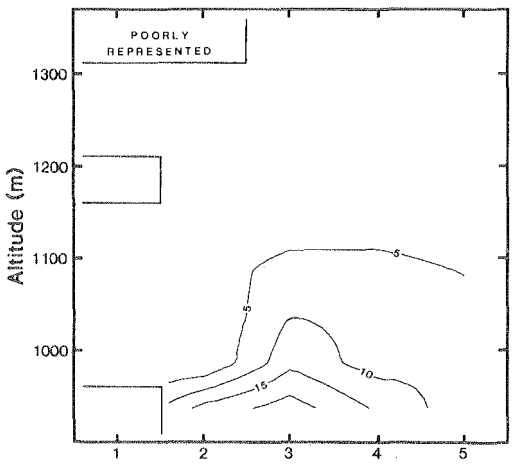
Observed Probability of Occurrence



Expected Probability (from Binomial GLM)

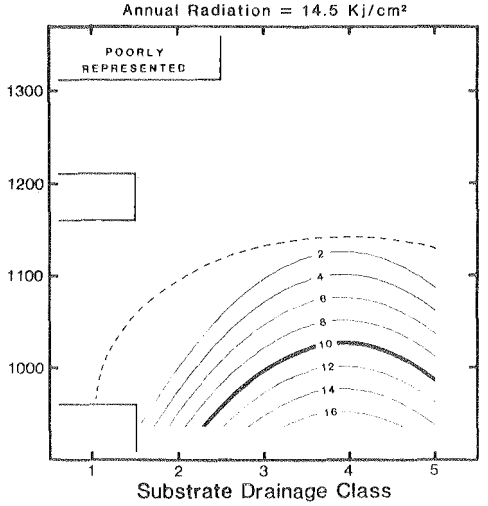


Observed Percentage Cover (Smoothed)

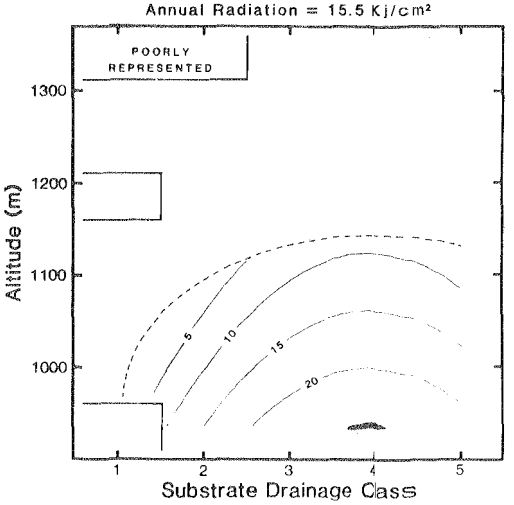


Expected Cover (from Normal Model)

Annual Radiation = 14.5 Kj/cm²

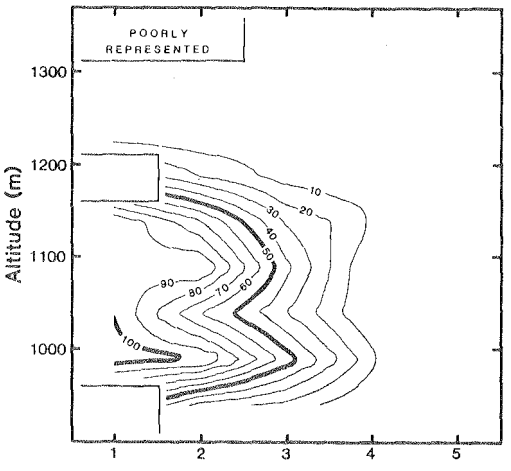


Annual Radiation = 15.5 Kj/cm²

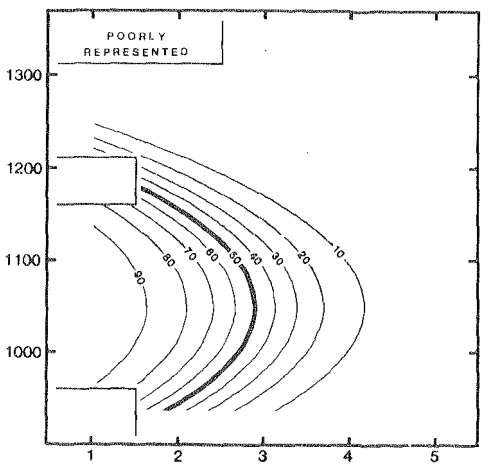


GLEICHENIA ALPINA

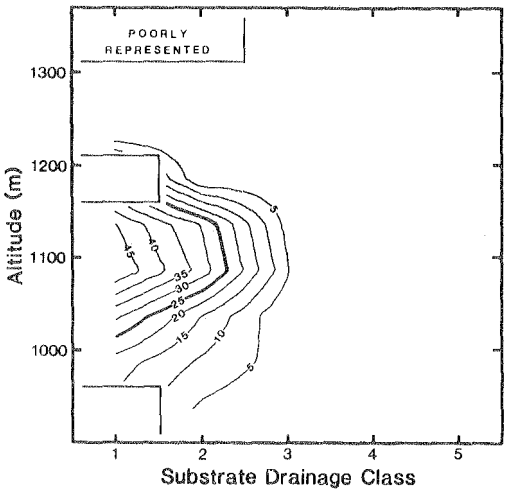
Observed Probability of Occurrence



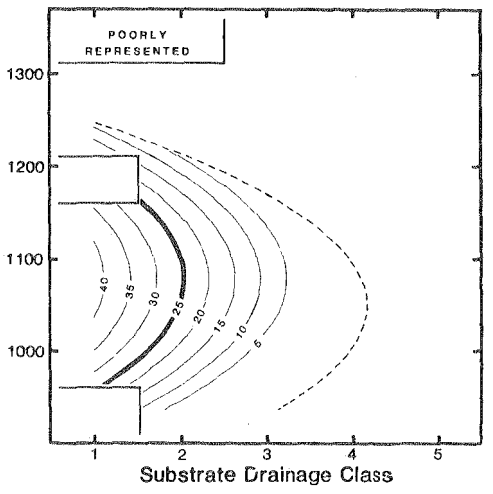
Expected Probability (from Binomial GLM)



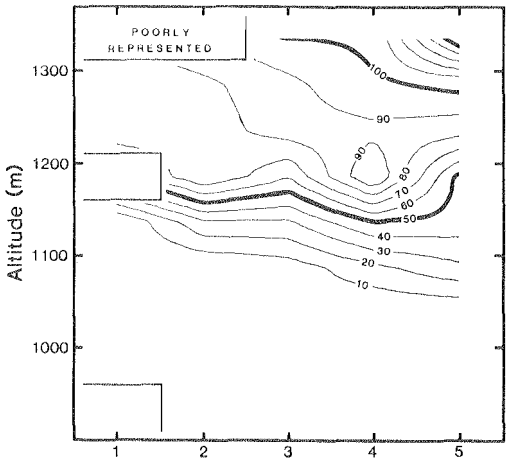
Observed Percentage Cover (Smoothed)



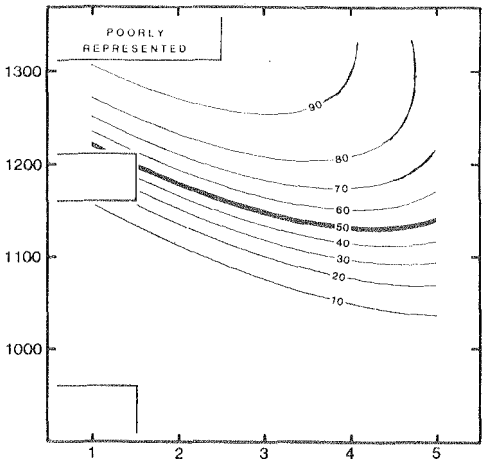
Expected Cover (from Normal Model)



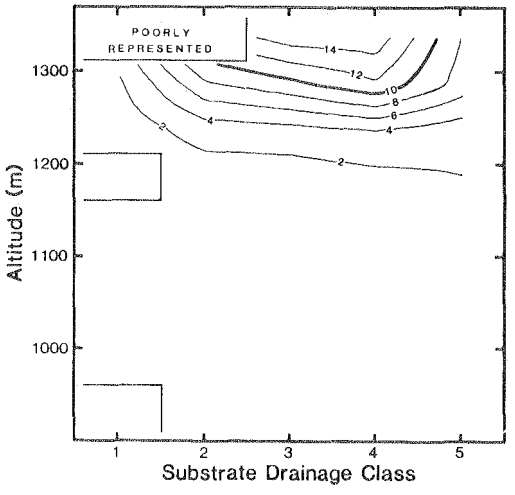
Observed Probability of Occurrence



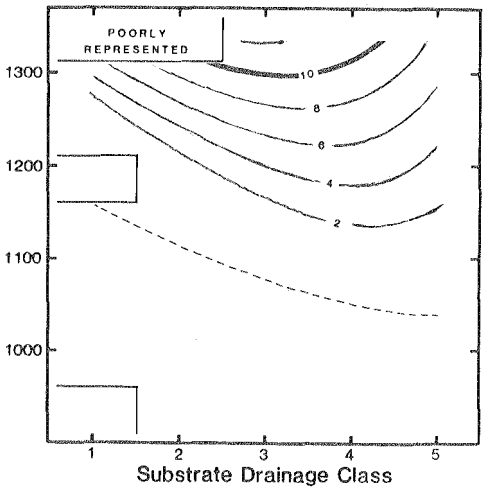
Expected Probability (from Binomial GLM)



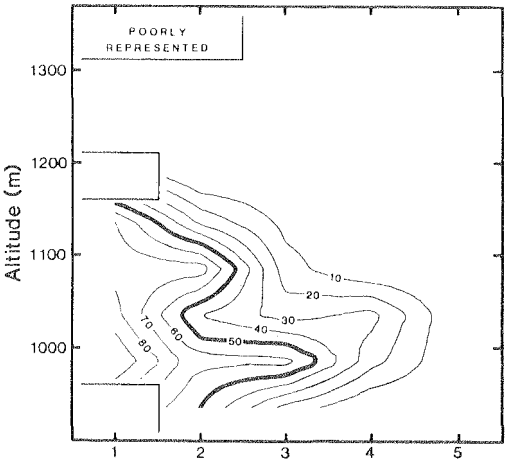
Observed Percentage Cover (Smoothed)



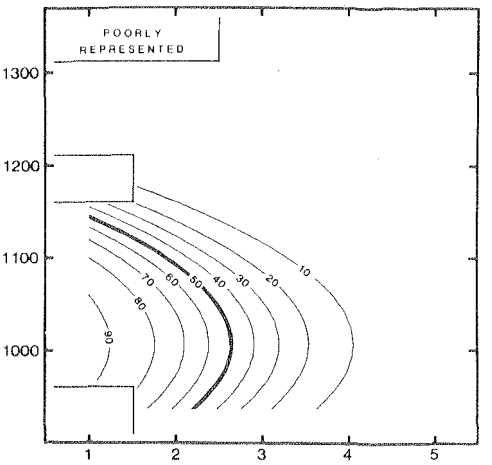
Expected Cover (from Normal Model)



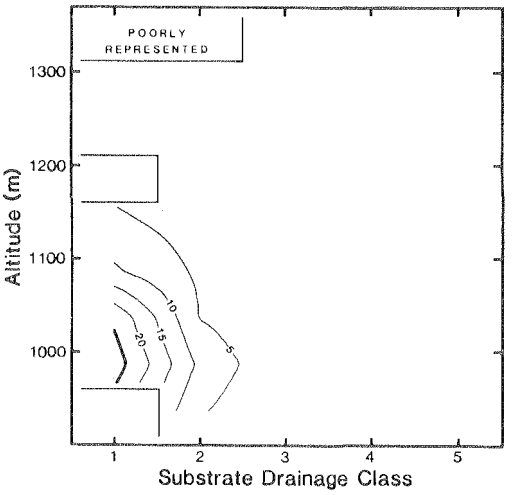
Observed Probability of Occurrence



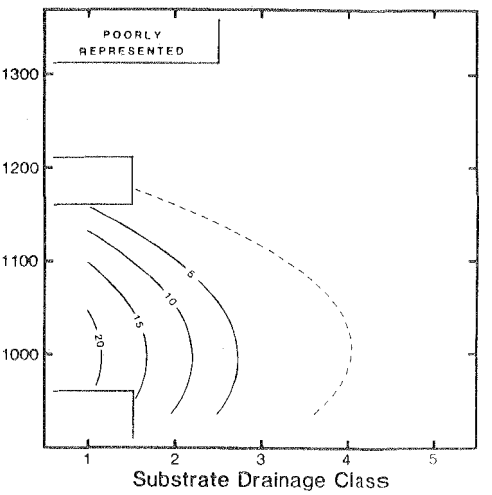
Expected Probability (from Binomial GLM)



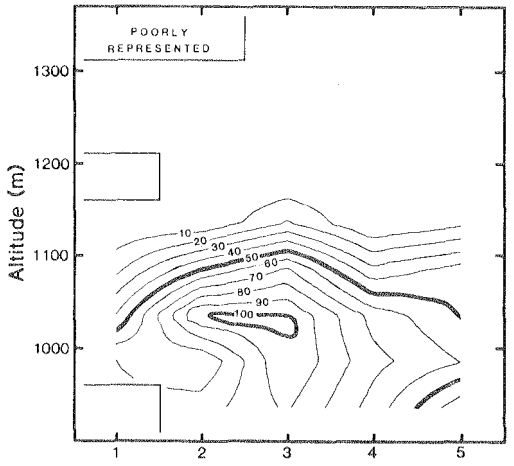
Observed Percentage Cover (Smoothed)



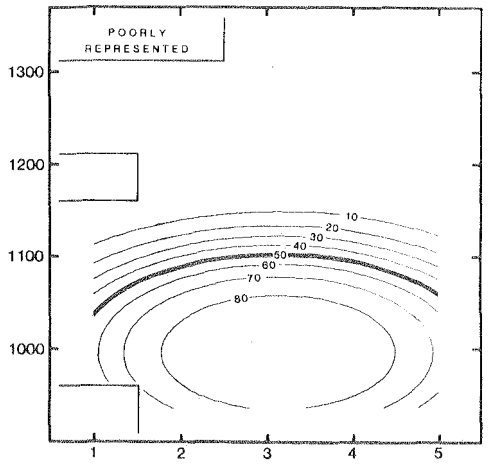
Expected Cover (from Normal Model)



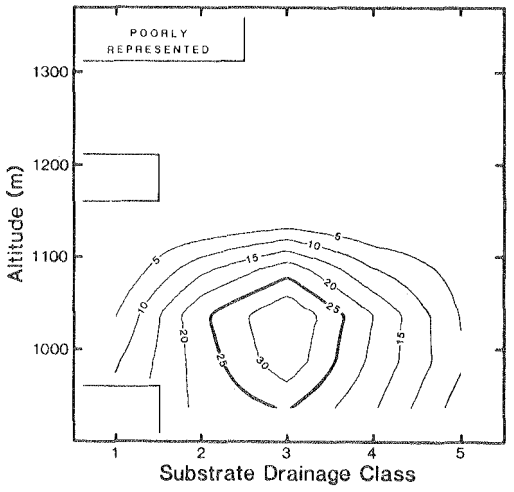
Observed Probability of Occurrence



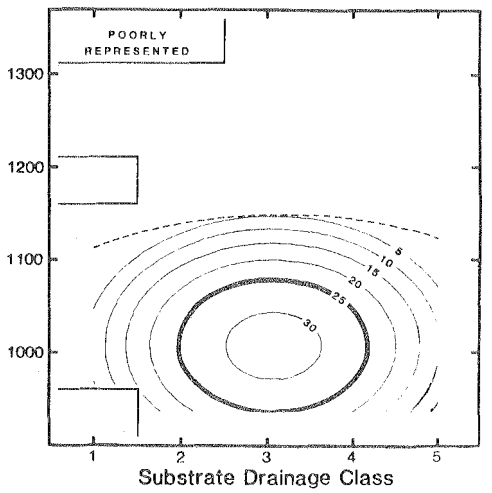
Expected Probability (from Binomial GLM)



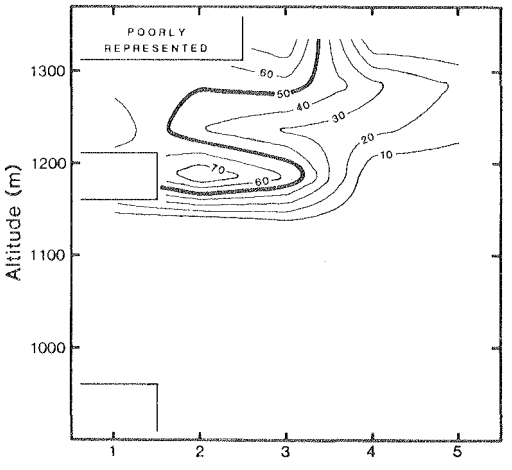
Observed Percentage Cover (Smoothed)



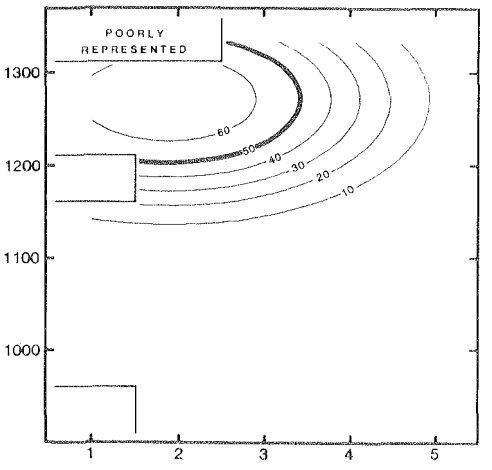
Expected Cover (from Normal Model)



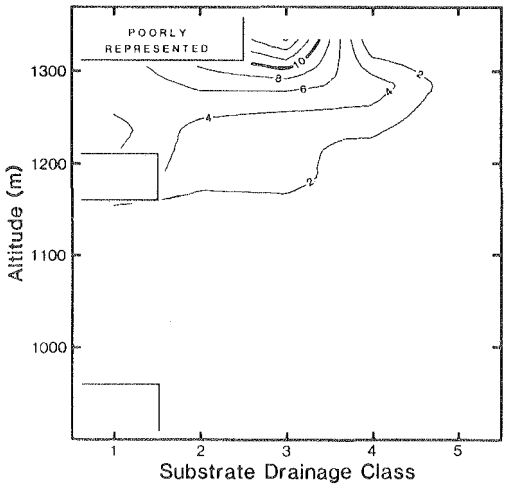
Observed Probability of Occurrence



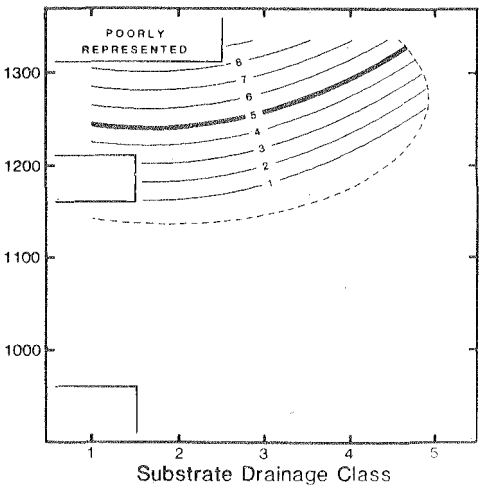
Expected Probability (from Binomial GLM)



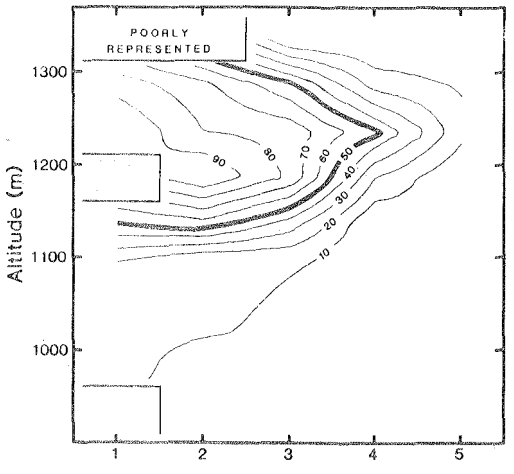
Observed Percentage Cover (Smoothed)



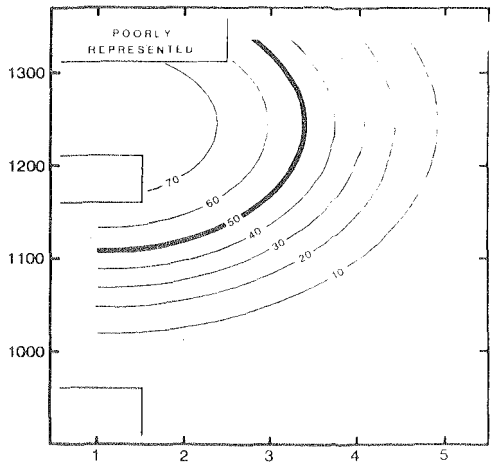
Expected Cover (from Normal Model)



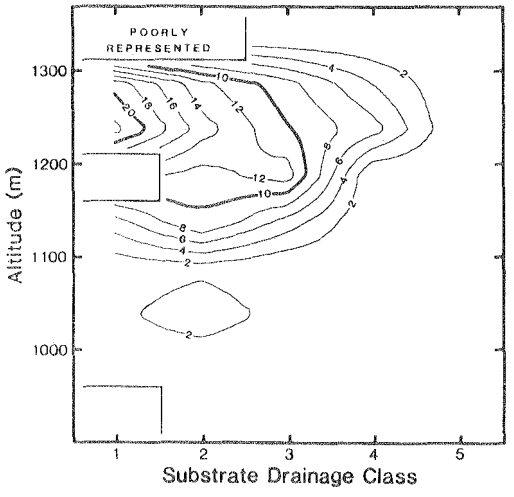
Observed Probability of Occurrence



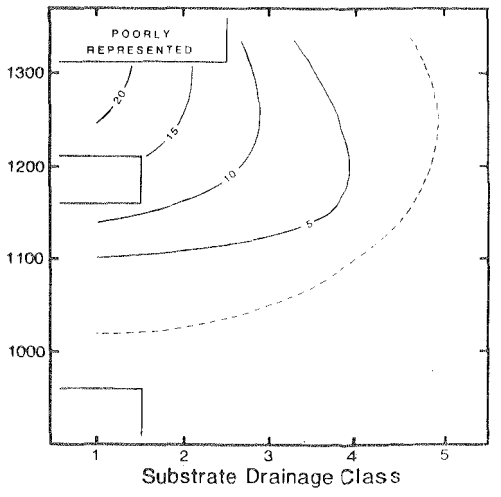
Expected Probability (from Binomial GLM)



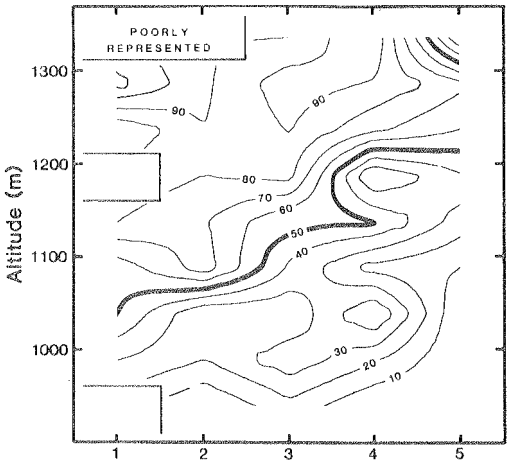
Observed Percentage Cover (Smoothed)



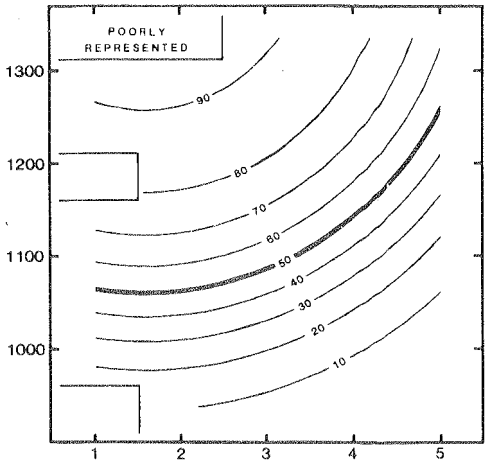
Expected Cover (from Normal Model)



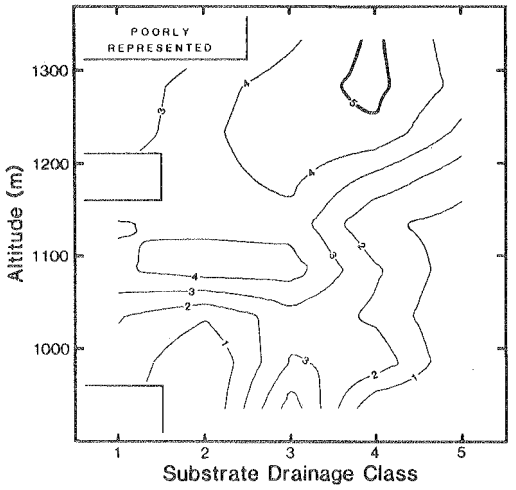
Observed Probability of Occurrence



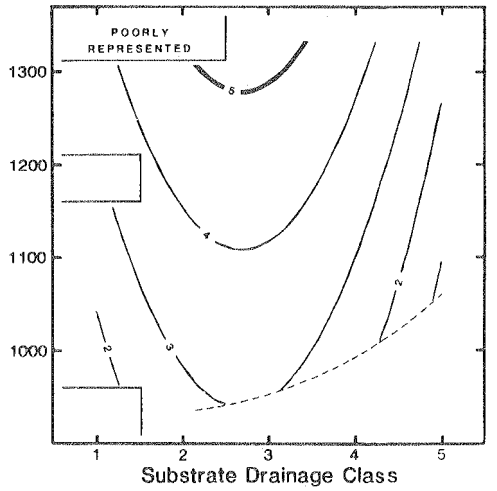
Expected Probability (from Binomial GLM)



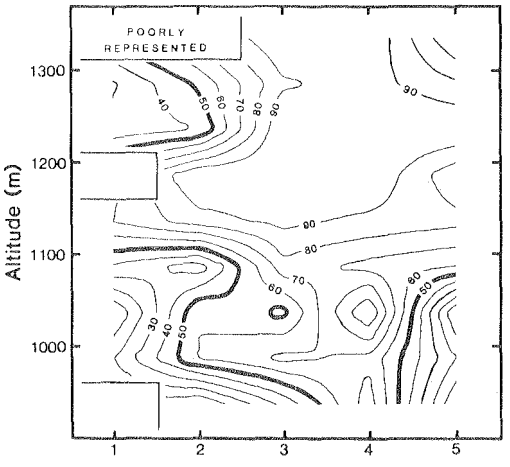
Observed Percentage Cover (Smoothed)



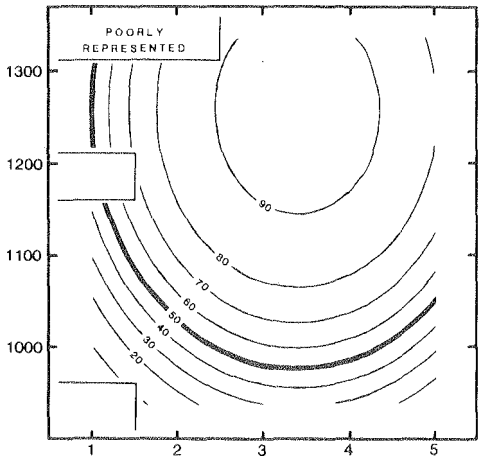
Expected Cover (from Normal Model)



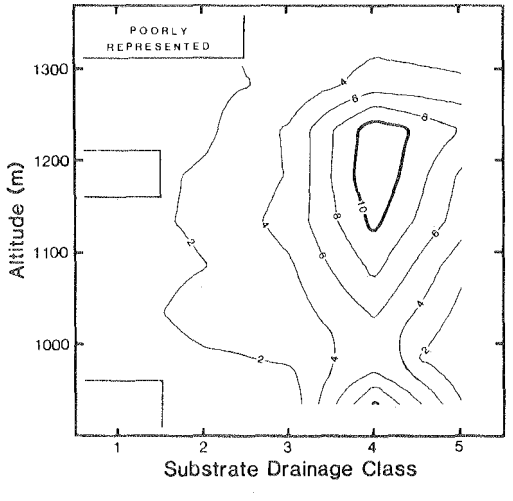
Observed Probability of Occurrence



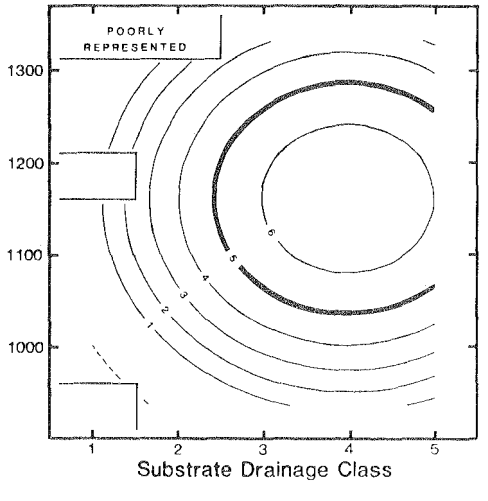
Expected Probability (from Binomial GLM)



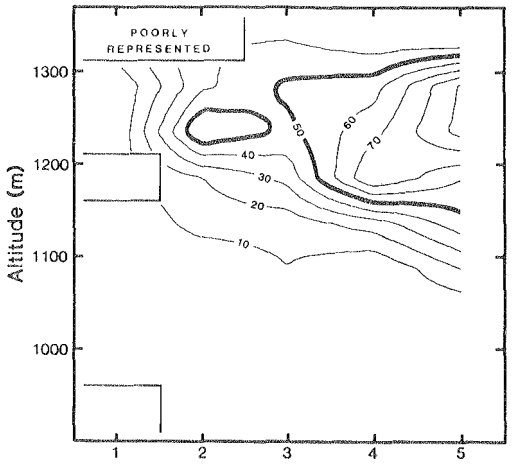
Observed Percentage Cover (Smoothed)



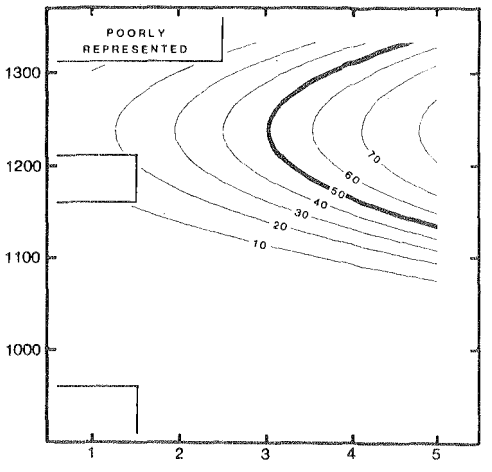
Expected Cover (from Normal Model)



Observed Probability of Occurrence



Expected Probability (from Binomial GLM)



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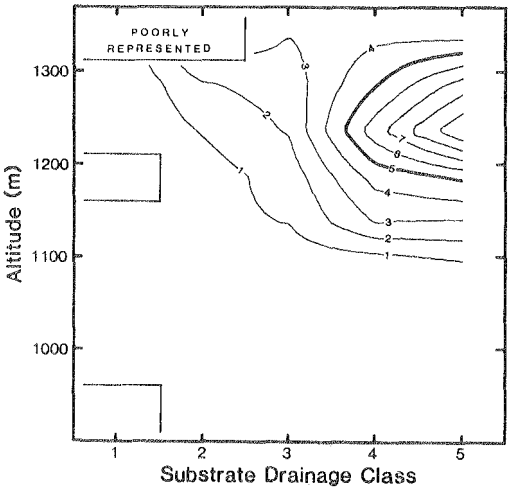

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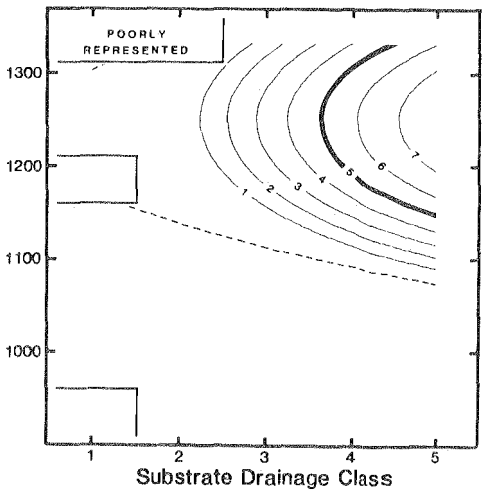

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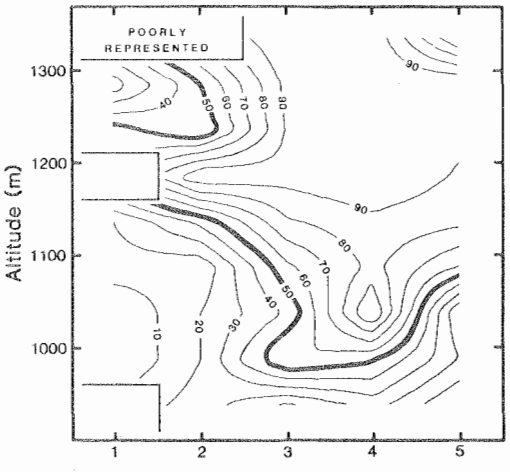
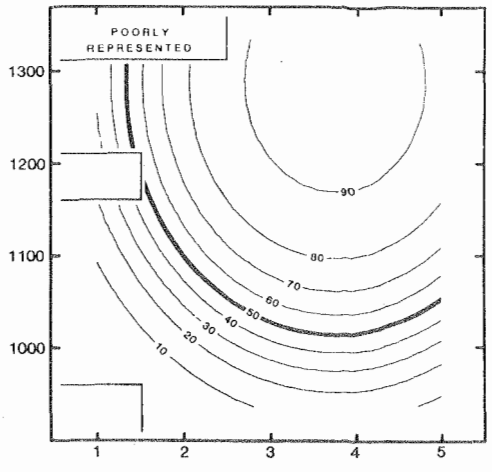


Expected Probability (from Binomial GLM)



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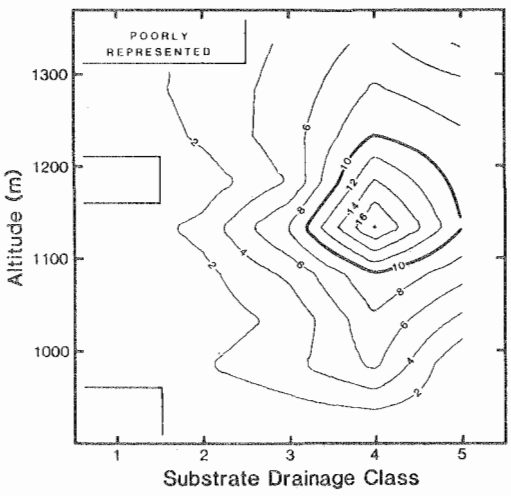

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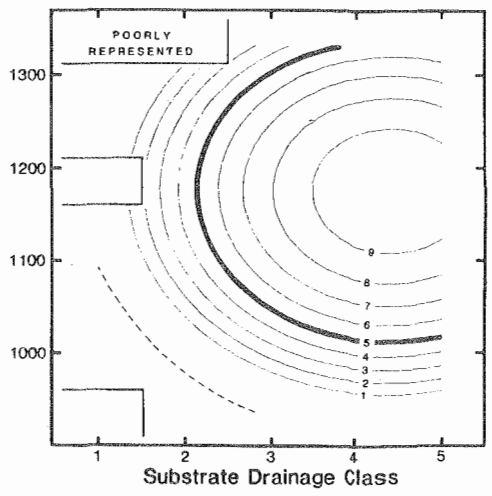

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